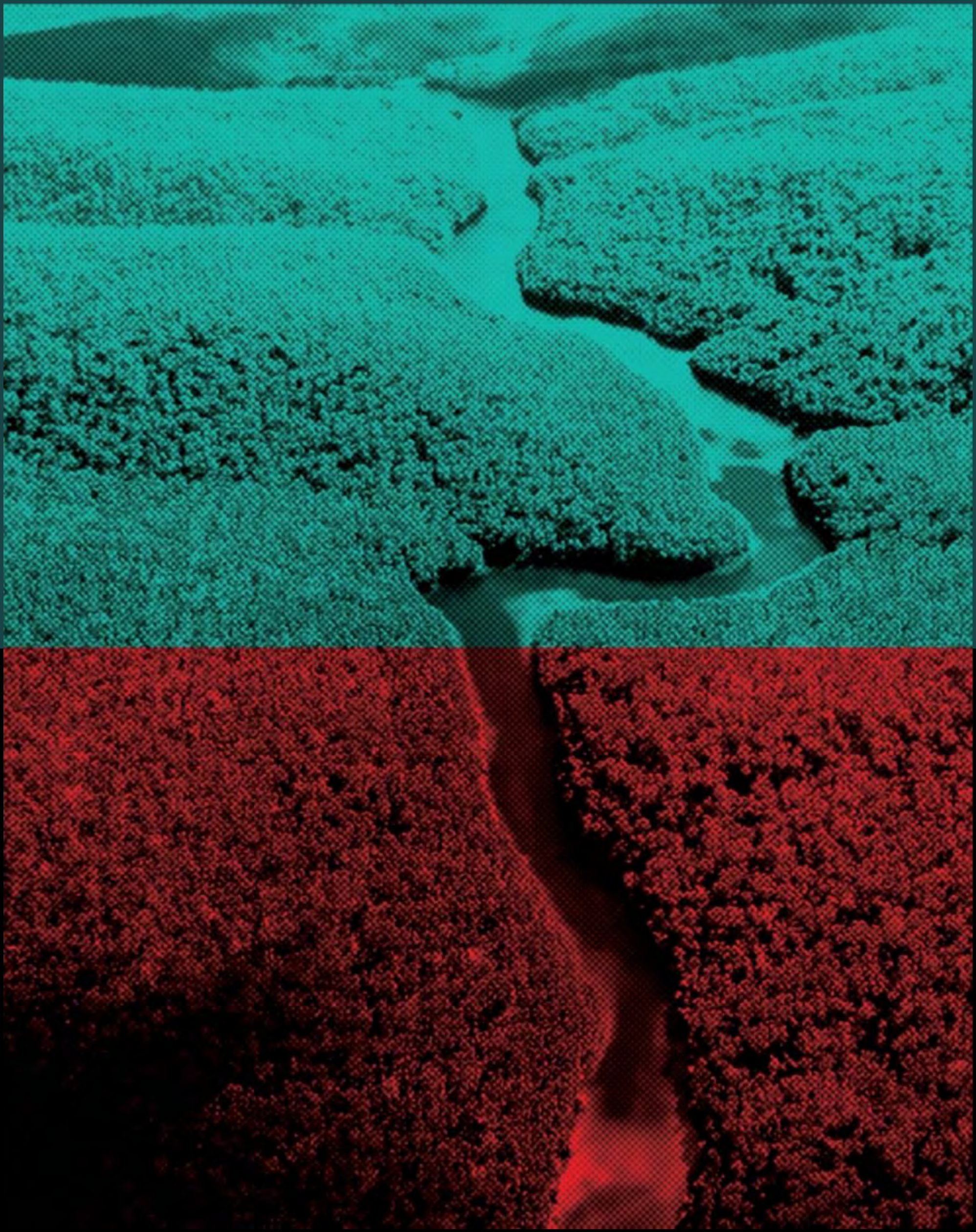
Science Panel for the Amazon

Amazon Assessment Report 2021

PART I



THE AMAZON WE WANT

Science Panel for the Amazon

SUSTAINABLE DEVELOPMENT SOLUTIONS NETWORK
A GLOBAL INITIATIVE FOR THE UNITED NATIONS

About the Science Panel for the Amazon (SPA)

The Science Panel for the Amazon is an unprecedented initiative convened under the auspices of the United Nations Sustainable Development Solutions Network (SDSN). The SPA is composed of over 200 preeminent scientists and researchers from the eight Amazonian countries, French Guiana, and global partners. These experts came together to debate, analyze, and assemble the accumulated knowledge of the scientific community, Indigenous peoples, and other stakeholders that live and work in the Amazon.

The Panel is inspired by the Leticia Pact for the Amazon. This is a first-of-its-kind Report which provides a comprehensive, objective, open, transparent, systematic, and rigorous scientific assessment of the state of the Amazon's ecosystems, current trends, and their implications for the long-term well-being of the region, as well as opportunities and policy relevant options for conservation and sustainable development.

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Part I

The Amazon as a Regional Entity of the Earth System

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FOREWORD

The Amazon Assessment Report is a marvel of scientific accomplishment and collaboration. Most of all, it is a result of the profound dedication of more than 200 scientists from the Amazon Basin nations to the well-being of the peoples and biodiversity of this unique part of the world. The Amazon merits every superlative thrown its way: unique, irreplaceable, mega-diverse, invaluable, and gravely endangered. The Science Panel for the Amazon has not only provided us with the most comprehensive and compelling scientific portrait of the Amazon ever produced, but has also provided a roadmap to the Amazon's survival and thriving. They show us, in short, the pathway to the Amazon We Want.

My colleague Emma Torres and I, and our fellow members of the UN Sustainable Development Solutions Network (SDSN), are deeply grateful and indebted to the scientist-authors of this volume for the profound care, scientific knowledge, and dedication that they put into this remarkable volume. When Emma and I helped to launch the Science Panel for the Amazon more than a year ago, in the midst of the COVID-19 pandemic, we envisioned that the region's leading scientists would produce a policy report to set guidelines for the Amazon's sustainable development. The scientists of course produced that, but they also produced something vastly greater. They delivered a *magnum opus*, a compelling narrative that begins with the ancient and formative geology of the Amazon Basin and that brings us to the present day, with powerful policy proposals for a new Amazon bioeconomy based on a Living Amazon Vision that "aims to transform the 'life-blind' economic system into one that is 'life-centric.'

Along the way they include a dazzling array of topics to ensure a comprehensive treatment of the Amazon from every major perspective, including the Amazon as a "regional entity of the Earth System," the "anthropogenic changes in the Amazon" including deforestation, and the "solution space" of sustainable pathways for the Amazon Basin. The solutions include bioeconomy strategies, protection of Indigenous lands, restoration of degraded lands, and stronger sustainable relations between the Amazon forest and Amazonian cities.

Both the urgency and timeliness of the report must be emphasized. The urgency is apparent from the core scientific message of the study: the Amazon's ecosystems are not only invaluable but are also gravely imperiled. Because of past deforestation and land degradation, the Amazon may well be close to a tipping point in which major ecosystems of the Amazon would irreversibly collapse or be persistently degraded.

The timeliness results from the fact that the world's nations are finally recognizing the imminent dangers facing the Amazon and the tropical rainforest regions of Africa and Asia. At COP26, more than 130 national governments signed on to a Glasgow Leaders' Declaration on Forests and Land Use, in which they promise to "halt and reverse forest loss and land degradation by 2030." At the same time, public and private sources together pledged more than $10 billion for this cause, with yet more funding to be mobilized. These governments have recognized, finally, that there can be no solution to climate change without ending deforestation and restoring degraded lands, in conjunction with transforming the global energy system to zero-carbon energy sources.

Even as the Assessment Report is being launched, the transformative importance of the Science Panel for the Amazon is already being recognized by governments in the region and by key international development agencies and institutions. This report and the ongoing work of the SPA will be taken up by the Leticia Pact that brings the region's leaders together to protect the common heritage of the Amazon, and by the

Amazon Cooperation Treaty Organization. Also, leading scientists working in other critical ecosystems, including the Congo Basin and the tropical forests of southeast Asia, are looking to the SPA for inspiration and guidance on how to carry out similar scientific collaborations and initiatives in those ecosystems as well.

Let us therefore savor the remarkable scientific insights gathered in this study, and commit as well to act upon the urgent messages of the SPA. If we act decisively and cooperatively, with the Amazon Basin countries cooperating closely and the rest of the world joining in urgent support of the Amazon, we can achieve the SPA's vision of "a healthy, standing forest and flowing rivers bioeconomy based on exchange and collaboration between local and Indigenous knowledge, science, technology, and innovation."

Jeffrey Sachs
SPA Convener

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We are profoundly grateful to the SPA Strategic Committee. Your distinguished leadership has been most valuable in providing strategic guidance to the work of the panel.

We are grateful to the members of the Technical Secretariat. This Assessment would not have been possible without their diligent efforts and dedication.

We also wish to express our profound gratitude to the peer reviewers who helped improve and clarify the Report, and to the many stakeholders who provided invaluable input through the public consultation as well as by other means.

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In gratitude,

Jeffrey Sachs	Emma Torres	Carlos Nobre	Andrea Encalada
Convener	Strategic Coordinator	Co-Chair	Co-Chair

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INTRODUCTION

The Amazon Basin holds the most extensive rainforest in the world (~5.8 million km^2), and the largest river, which flows four thousand kilometers from the Andes to meet the Atlantic, carrying more water than any other river (~220,000 m^3/s). Billions of years of geologic and climatic changes and millions of years of biological evolution resulted in a highly heterogeneous region sheltering an unparalleled, vast, but still mostly unknown biodiversity. The Amazon rainforest is a vital ecosystem for the entire planet and part of the irreplaceable heritage for all humanity. The Amazon Basin is also home to Indigenous peoples that co-evolved with biodiverse ecosystems for more than ten thousand years, driving the emergence of a vast biocultural diversity.

Notwithstanding, the Amazon and its inhabitants have been historically threatened by a resource-based development model with a monetary-centric vision that causes ecosystem destruction while maintaining inequalities and violence. This model has been associated with a tremendous loss of intact, diverse forests and degradation of terrestrial and aquatic ecosystems by deforestation, non-natural fires, logging, natural resources exploitation, and pollution. Together with global climate change, these activities are pushing the Amazon towards a tipping point beyond which lies irreversible loss of the rainforest and its biodiversity, severely compromising human well-being. Halting deforestation and ecosystem degradation and finding alternative pathways towards the sustainable development for the Amazon are a priority under this critical scenario.

Despite the existing wealth of scientific and socio-environmental knowledge on the Amazon, there are still significant gaps in our understanding; this affects our ability to guide conservation strategies and support science-based decision-making processes, and demands great scientific and technological efforts to overcome. For instance, although scientists have described thousands of species in the Amazon, the full dimensions of Amazonian biodiversity remain vastly underestimated. Furthermore, despite the great effort of scientists to quantify carbon emissions and ecosystem productivity, limited data on the potential effects of CO_2 fertilization on photosynthesis and water use by trees restrict our understanding of forest resilience in the face of climate change. Finally, notwithstanding the enormous diversity of knowledge systems connected to the Amazon´s cultural and biological diversity, there are limited investigations into how these systems generate, transmit, and use such knowledge.

Under the auspices of the UN Sustainable Development Solutions Network (SDSN), over 200 scientists from the Amazon and who study the Amazon have come together to form the unprecedented Science Panel for the Amazon (SPA). They brought together their knowledge and experience to produce a Scientific Assessment of the state of the diverse ecosystems, land uses, and environmental changes in the Amazon and their implications for the region and other parts of the world. The challenge was unprecedented, to produce the first full-fledged scientific report carried out for the entire Amazon Basin and its various biomes, including an opportunity to develop a new, sustainable paradigm that ensures that the forest is worth far more standing than cut down, and that freshwater resources are managed sustainably. The well-being of those who inhabit the planet today and of generations to come depends on conservation of the Amazon.

This Report is divided into three main parts, each containing four Working Groups and together totaling 34 chapters:

I - The Amazon as a Regional Entity of the Earth System
II - Social-Ecological Transformations: Changes in the Amazon
III - The Solution Space: Finding Sustainable Pathways for the Amazon

Part I addresses an undisturbed - or with very low human-induced disturbance –Amazon Basin through the geologic, climatic, and ecological evolution of terrestrial and aquatic ecosystems and biodiversity. It explores why the Amazon rainforest is an important contributor to regional and global biogeochemical cycles, such as the carbon cycle and major nutrient cycles, and synthesizes the main mechanisms which operate in the physical hydroclimate of the Amazon. Part I ends by exploring human presence in the Amazon, highlighting the critical role of Indigenous peoples and local communities (IPLCs) in the sustainable use and conservation of Amazonian biodiversity and the consequences of European colonization for these populations.

Part II focuses on increasing anthropogenic changes in the Amazon, mainly from the 1960s to the present day. From the 1960s onwards, the Amazon experienced the most profound socio-environmental transformation in its history. Part II starts by reviewing the current situation of the diverse peoples who live, move, and work in the Amazon region, putting into context the changes in global policies and deep regional integration into the world economy. Such integration moved the Amazon to the top tiers in global exports of beef, iron, gold, timber, cocoa, and soy, which occurred in the context of highly unequal societies, threatening the rainforest, aquatic ecosystems, and the survival of IPLCs. National conservation policies are discussed as a counterforce to protect biodiversity, cultural diversity, and the territorial rights of IPLCs. Next, the chapters analyze the current reality of a highly complex and dynamic mix of rural and urban activities, including the formal, informal, and clandestine economies that drive deforestation. This includes the expansion of pastures and croplands, and ecosystem degradation such as pollution and forest fires. The cumulative impacts of multiple drivers of forest loss and terrestrial and aquatic degradation on biodiversity, climate, and the carbon cycle are described from the local to the global perspective, including their cascading effects on agriculture, hydropower generation, and human health and well-being. Last but not least, Part II ends with a warning of the imminent risk of crossing a tipping point due to ongoing land conversion and climate change; beyond this point, continuous forests can no longer exist and are replaced by highly degraded ecosystems.

Part III of the report focuses on solutions, presenting recommendations based on scientific and traditional knowledge, guided by the principles and values of the *Living Amazon* vision. This vision proposes a sustainable development model for the Amazon that is socially just, inclusive, and ecologically and economically flourishing. It recognizes the role of the Amazon in the 21st Century and the need for economies that can sustain ecological integrity and diversity, protect terrestrial and aquatic ecosystems, restore and remediate impacted ecosystems, empower Amazonian people, protect human rights and the rights of nature, and promote human-nature well-being. The solutions proposed are based on three pillars:

1) Conservation, restoration, and remediation of terrestrial and aquatic systems
2) Development of an innovative, healthy, standing forests, flowing rivers bioeconomy; addressing policies and institutional frameworks for human-environmental well-being and biodiversity protection; ingenuously combining the knowledge of IPLCs and scientific knowledge; and investing in research, marketing, and production of Amazonian socio-biodiversity products
3) Strengthening Amazonian citizenship and governance, which includes the implementation of bio-regional and bio-diplomatic governance systems (environmental diplomacy) to promote better management of natural resources and strengthen human and territorial rights

More than ever, the SPA Assessment is a timely opportunity to show the connection between human well-being and nature to a broad audience, including decision makers. The sustainable functioning of the Amazon's ecosystems guarantees the safety of the people who live in the Amazon and its surroundings, and supports planetary health. The SPA Report urges decision makers and all societies to act now to prevent further devastation in the region. Key outcomes of this unprecedented scientific report are new recommendations for a sustainable Amazon, which can serve as models for all tropical forests. Given the rapid transitions experienced by the Amazon and the world, there is great need for better communication between policy makers and the scientific community, including consensus on several key issues. Although threats and their administration fall first and foremost to Amazonian nations, the responsibility of saving the Amazon is global. What transpires in the Amazon in one country affects the Amazon in all countries, and what happens in the Amazon affects the entire world. Therefore, actions within the Amazon itself convergent with global actions to stop human-induced Amazon crises are urgent.

Carlos Nobre	Mercedes Bustamante
SPA Co-Chair	*SPA Science Steering Committee*

Amazon Assessment Report 2021

Chapter 1

Geology and geodiversity of the Amazon: Three billion years of history

Vista aérea da Terra Indígena Yanomami (Foto: Bruno Kelly / Amazônia Real)

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Graphical Abstract

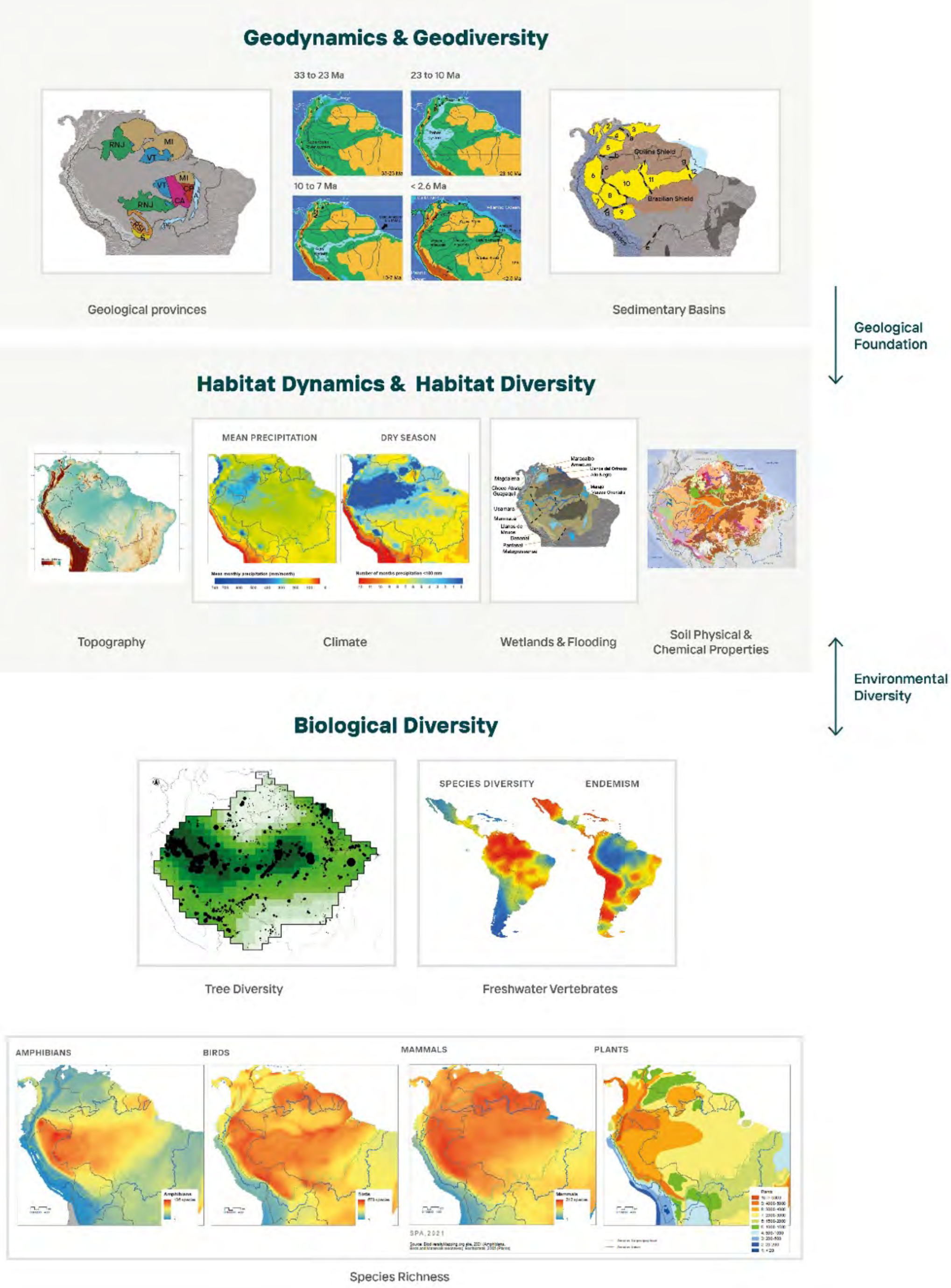

Figure 1.A Geodynamics and geodiversity (top panel) of the Amazon, which form the geological foundation for habitat dynamics and diversity (middle panel), and the environmental heterogeneity and gradients that drive biological diversity (bottom panel). Image sources: top panel, from left to right, geologic provinces from Macambira *et al.* (2020), and the uplifting Andes, sedimentary basins, and stable cratons from Fuck *et al.* (2008), landscape and drainage evolution sequence through the past 30 Ma from Hoorn *et al.* (2010b), dynamic Andes and sedimentary basins and stable cratons from Albert *et al.* (2018); middle panel, from left to right, topography from NASA Earth Observatory, precipitation and seasonality from Restrepo-Coupe *et al.* (2013), wetlands and flooding from Albert *et al.* (2018), soil from Quesada *et al.* (2011); bottom panel, from left to right, species richness from Plant-Talk.org (https://www.plant-talk.org/ecuador-yasuni-biodiversity.htm), tree diversity from Hoorn *et al.* (2010b), freshwater vertebrates from Albert *et al.* (2020).

Geological History and Geodiversity of the Amazon

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Key Messages

- Modern Amazonian landscapes can only be understood in the context of geological and climatic processes operating over hundreds of thousands to billions of years.
- The subdivision of the Amazon into craton versus Andes-influenced landscapes and soils is the result of a unique geologic history that was determined by the interplay of plate tectonics, climate, dynamic topography, and sea level change. Together these factors created an exceptionally high geodiversity and diverse hydrological landscape.
- Amazonian geodiversity arises from the heterogeneous distribution of lithologies in the geological substrate and edaphic (soil) conditions at many spatial scales, under the perennial influence of varied hydrological and biological process, at the surface and subsurface.
- It took hundreds of millions of years for the Amazon to develop the rich tapestry of landforms, soils, and ecosystems we see today, but humans degrade these unique ecosystems at a much faster rate. Decisions should be made to avoid further degradation and consider the time necessary for the Amazon to recover, which, if at all, will not be on a human-relevant timescale.

Abstract

The Amazon hosts the most diverse tropical forest on Earth. But underneath, the Amazon also comprises an exceptionally geodiverse landscape, marked by the towering Andes in the west, highland plateaus with dramatic escarpments in the east, and the Amazon River traversing the region as a major artery. The region's exceptional geodiversity and biodiversity have shaped one another through time, as geological forces created the diverse soils, biotas, and hydrological landscapes of the modern Amazon. In this chapter we explore how these features evolved over a three-billion-year history, and show that periods of continental breakup followed by mountain building ultimately led to the characteristic subdivision of the western and eastern Amazon, while also generating a wealth of ore deposits, oil and gas reserves, and freshwater aquifers. The modern landscape was initiated after the supercontinental breakup that separated the continents of South America and Africa (c. 100 million years ago, or Ma), leading to the opening of the Atlantic Ocean and the gradual uplift of the Andes Mountains. However, the Central and Northern Andes only reached their present altitude after accelerated uplift during the Neogene (c. 20 Ma) due to changes in Pacific plate motions. Together with a rise in global temperatures and sea level during the mid-

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dle Miocene (c. 17–15 Ma), the uplift of the Andes prompted radical changes in the Amazonian paleogeography, paleoclimate, and paleoenvironments, resulting in the creation of a large mega-wetland known as the Pebas System. The rise of the Andes further caused an eastward tilt in sedimentary basins that resulted in drainage changes and the formation of the transcontinental Amazon River (c. 10–4.5 Ma). These geological changes form the basis of the present west to east trending gradient, which is reflected in the geomorphology, lithology, and geochemistry, and explains contrasting weathering rates and nutrient composition across the Amazon. Conversely, the diverse hydrologic and geochemical regimes affect physical and chemical weathering, erosion, and deposition, feeding the geological subdivision of the Amazon. Global climate change also played a role by modifying Amazonian geomorphology and river base levels. Periods of global warming and high sea level, such as in the middle Miocene, inundated the Amazon with marine water, whereas global cooling, in the late Miocene (c. <11 Ma) and culminating in the Quaternary (c. <2.6 Ma), led to glacier formation in the high Andes and global sea level fall. The latter resulted in deep incised valleys and ria-like relict river patterns that are still visible in the Amazonian landscape today. During the interglacials, glacier melt also impacted the Amazonian landscape through megafan deposition at the interface between the Andes and Amazon. Looking into the future, and with knowledge of deep time history in mind, the anthropogenic effect of increasing atmospheric CO_2 on climate today may lead to an ice-free world in which renewed — fast rising — global sea level is likely and would result in an inundation of part of the Amazon, similar to the scenario last seen in the middle Miocene. In short, the geographic position of the Amazon, with its unique geological and climatic history, has created an unparalleled geodiversity, the foundation for the evolution of life and its unmatched biodiversity today. The rates of change induced by anthropogenic activity may outpace anything seen in geological and vegetation records and lead us to an uncertain future.

Keywords: Geodiversity, Amazon craton, aquifers, Andean uplift, megafans, soils, hydrology, ores, Andes, Amazon River, mega-wetland, Pebas

1.1 Introduction

The Amazon is a globally unique region of exceptional geodiversity (Gray 2008; Bétard and Peulvast 2019), arising from variations in underlying rocks and mineral resources, emergent topography and surface relief, and heterogeneous distributions of surface and subsurface water flows (hydrology) and soil types (edaphic conditions) (Figure 1.1). Despite the lack of a formal consensus on the geographical division of the Amazon, we choose to separate the Amazon into the eastern and western Amazon based on their surface expressions. The geology of these regions is distinct; the eastern Amazon is dominated by Precambrian shields with Paleozoic sedimentary basin in between and occupy a relatively small area; the western Amazon is largely dominated by Cenozoic sedimentary basins, with Precambrian shields spatially restricted towards the northern and southern limits. These landscapes reflect the geology well, with the shield areas generally being marked by plateaus (above c. 250 m elevation), which we refer to as the upland regions in both the eastern and western Amazon. Instead, the landscapes across the Cenozoic sedimentary basins are generally marked by smooth, low-lying topography (below c. 250 m) which we nominate as the Amazon lowlands. The western Amazon margin is marked by the Andean cordillera and its foothills, which together rise upwards of 3–6 km in elevation. As we shall learn in this chapter, these distinct geographical regions also condition continental-wide patterns in the chemistry and nutrient content of surface waters, groundwaters, and soils, affecting hydrology, tree composition, forest growth rates, and biodiversity (ter Steege *et al.* 2006; Hoorn *et al.* 2010a, b; Higgins *et al.* 2011; Quesada *et al.* 2011, 2012).

The origins of these diverse Amazonian areas and landscapes need to be traced to a lengthy and dynamic history of geological evolution ruled by plate tectonics (Box 1.1), climate change, and sea level fluctuations, extending over millions to billions of years. The oldest Amazonian rocks were formed during the Meso to Neoarchean era (3.0–2.5 billion years ago [Ga]) (Macambira *et al.* 2020). This Archean core was reshuffled by plate tectonics through the amalgamation of several terranes from c. 2.1 to 1.0 Ga, which gave origin to the Amazon Craton (Macambira *et al.* 2020). On top of this craton, some intracratonic sedimentary basins recorded sedimentation since the Ordovician (c. 485 million years ago [Ma]) and some still accumulate sediments today. Two other main geologic events fundamentally changed the Amazon region: the breakup of the final bridge between the South American and African continents (c. 100 Ma) (Figueiredo *et al.* 2007) and the (re)connection with North America (c. 12–3.5 Ma) (Montes *et al.* 2015; O'Dea *et al.* 2016). It is important to emphasize that the shift from craton- to Andes-dominated processes, after the opening of the South and Equatorial Atlantic during the late Early Cretaceous (c. 120–100 Ma) is a fundamental part in this history (Wanderley-Filho *et al.* 2010; Mora *et al.* 2010). It was during this later stage that today's west-to-east topographic gradients began to take form.

The Amazon is also wealthy in terms of its many mineral and hydrocarbon resources, in particular metal ores, oil and gas, and freshwater aquifers. Metal ores such as iron (Fe), aluminum (Al), gold (Au), manganese (Mn), nickel (Ni) and tin (Sn) are common around the Precambrian shields and represent important export commodities. The genesis of these ores is closely related to the multibillion-year geological history of the Amazon (See section 1.2). Hydrocarbon reserves are abundant in the Subandean foreland basin of the western Amazon, with origins in the past 100 Ma. Freshwater aquifers underlie much of the lowland Amazon, being most heavily exploited in the Alter do Chão Formation in the eastern Amazon. These resources represent important potential sources of wealth; however, the environmental and sociopolitical impacts of their exploitation are highly contentious (See Chapters 10 to 15).

In this chapter we summarize the geological history of the Amazon, from its origins to the formation of contemporary landscapes. We use this geological narrative to explain the genesis of complex soils systems and hydrological regimes, as well as the distribution and abundance of the region's heterogeneous resources. A major objective of this chapter is to explain how geological, climatic, and hydrological processes have conspired over geological time to generate the geodiverse landscapes of the modern Amazon, and how these processes and landscapes ultimately set the stage for the evolution of the most species-rich biota on Earth.

Box 1.1 Earth and Plate Tectonics

The origin of Planet Earth is linked to the origin of our solar system, starting about 4.5 Ga. Geologists divide the Earth's history into four major divisions they call "EON" or "AEON," inspired by the Greek word αἰών (aiwṓn) that means eternity. The four Eons are Hadean, Archean, Proterozoic, and Phanerozoic. The hard shell of the Earth, known as the "Lithosphere," was formed by two processes over geological time. Initially, magmatic differentiation prevailed, or in simple words the solidification of magma. Later, the processes responsible for plate tectonics started. The rocks, which formed by magmatic differentiation, are the cores to which other, later geological terranes were added due to plate tectonics to form the cratons, supercratons, continents, and eventually, supercontinents (Harrison 2009; Hasui 2012; Hazen 2012).

Though no consensus exists, many authors propose plate tectonics had already started in the Mesoarchean (3.5–2.8 Ga), despite being different from present-day processes (Ernst 2009). For instance, during this Eon not much of the Earth's surface was solid rock; therefore, plate tectonics was not on a global scale like today but localized near the solid cores formed by magmatic differentiation. Once movement started, so did the formation of continental assemblages and the congregation of cratons, supercratons, continents, and supercontinents.

1.2 Three Billion Years of Amazon History in a Nutshell

1.2.1 Assembling a Continent: Cratonization

1.2.1.1 The cratonic core

The oldest core of the Precambrian shield of the Amazon is dated to between 3.0 and 2.5 billion years ago (Ga) and corresponds to the Carajás Province (Macambira *et al.* 2020; Figure 1.2.). The area of this core outcrops mostly in what today is the eastern Amazon, and is surrounded by younger crustal terranes, which were added from 2.1 to 1.0 Ga. The amalgamation of Paleo- to Mesoproteroizoic terranes around the older Carajás Province Archean core consolidated the so-called Amazon Craton. It occupies most of western Brazil, covering almost half the size of the Brazilian territory, extending also into several other South American countries, and is larger than the modern Amazon drainage basin (Hasui 2012 and references therein).

The Amazon Craton is subdivided into two exposed areas, or 'shields', the Guiana Shield in the north and the Central Brazilian Shield in the south (Figure 1.2.). These shields are separated by sedimen-

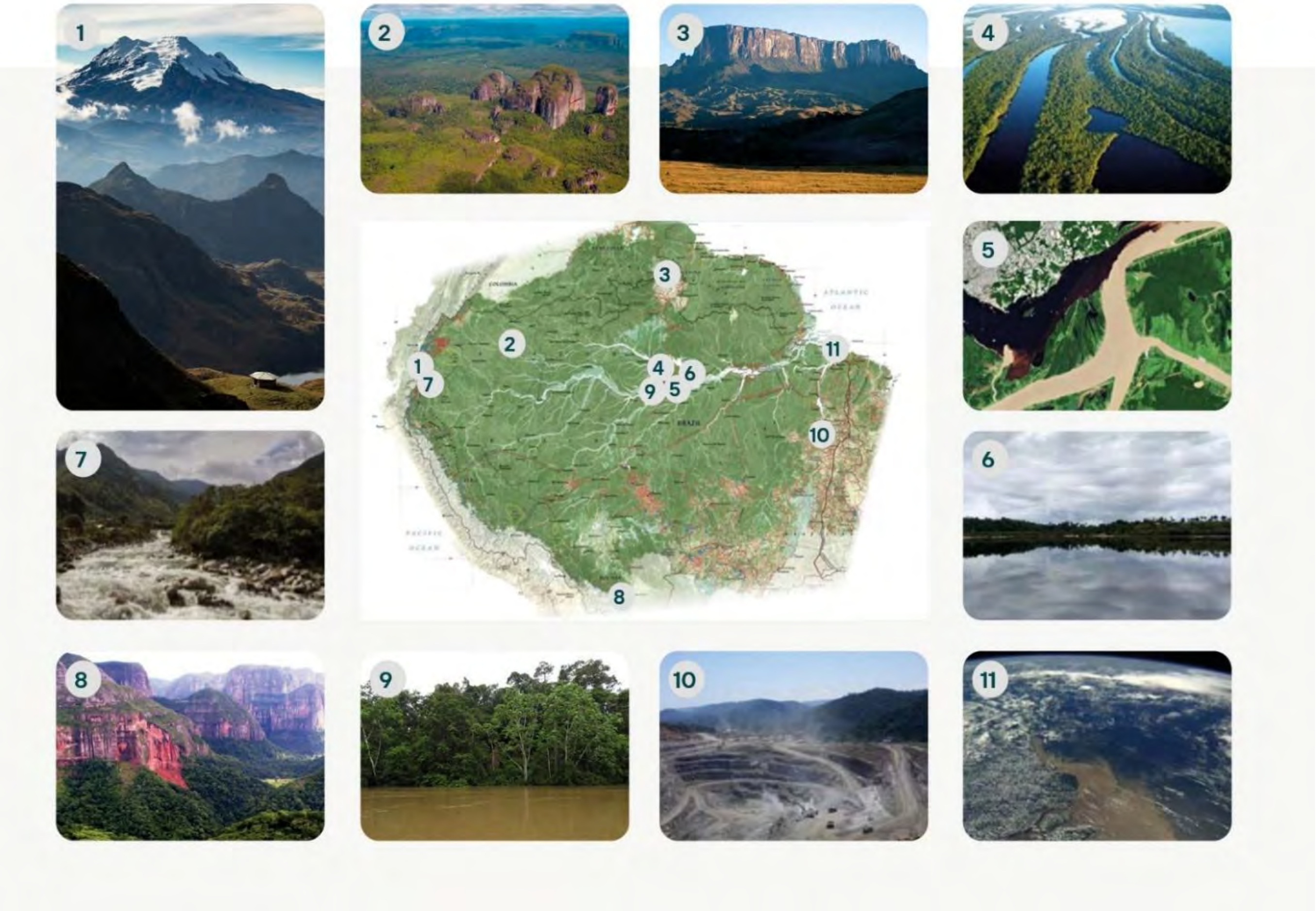


Figure 1.1 Photographic overview of the geology and geodiversity of the Amazon 1. The Andes in Ecuador (Esteban Suárez), 2. Chiribiquete (© Steve Winter), 3. Monte Roraima (Paulo Fassina), 4. Anavilhanas (Marcio Isensee e Sá / (o)eco), 5. Negro-Solimões River junction, contains modified Copernicus Sentinel data (2018) processed by ESA, CC BY-SA 3.0 IGO (https://creativecommons.org/licenses/by-sa/3.0/igo/), 6. Lowland river (Pedro Val), 7. Andean river (Esteban Suárez), 8. Amboro National Park (Pattrön), 9. Várzea near Manaus (Hans Ter Steege), 10. Salobo Copper Mine in the Carajás Province (Gustavo Melo), 11. Mouth of the Amazon River (*Foz do Amazonas*) (European Space Agency https://www.uu.nl/en/news/amazon-river-impacted-eutrophication-of-atlantic-ocean).

tary basins and cover about 40% of the Amazon. Alongside the Andes and associated sedimentary basins, the shields represent the most important geological setting of the continent, on which numerous geologic, surface, biologic, and climatic processes acted in parallel to produce the magnificent environmental diversity currently found in the Amazon.

1.2.1.2 Amalgamation of terranes

The history of the consolidation of the Amazon Craton is linked with supercontinents assembly, particularly with Rodinia and Columbia (Zhao *et al.* 2004; Nance *et al.* 2014), the latter being different to the country 'Colombia'. During this time, the proto-Amazon Craton (i.e., the Carajás Province) was located at the southern margin of Columbia, while new terranes were accreted along its margins. The Maroni-Itacaiúnas Province collided with the northeastern border of the proto-Amazon Craton, while the Central Amazon, the Ventuari-Tapajós and Rio Negro-Juruena provinces, accreted to the southwestern margins (Figure 1.2.A). These new terranes expanded the areal extent of the craton, enhancing its mineral richness with rare metals like gold. By that time, at least half of the geological substrate of Amazon had already been formed (Tassinari and Macambira 2004; Santos *et al.* 2008).

Due to their geographic position on a stable continental platform, the Proterozoic sedimentary basins within the Amazon Craton were protected against subsequent continental collisions. Hence their sedimentary content remained relatively undisturbed over extended time. An example is the geomorphological province of table-top structures known as the "pantepui" (Figure 1.2). These sandstone platforms, such as Mount Roraima on the Guiana Shield, were formed by mostly fluvial

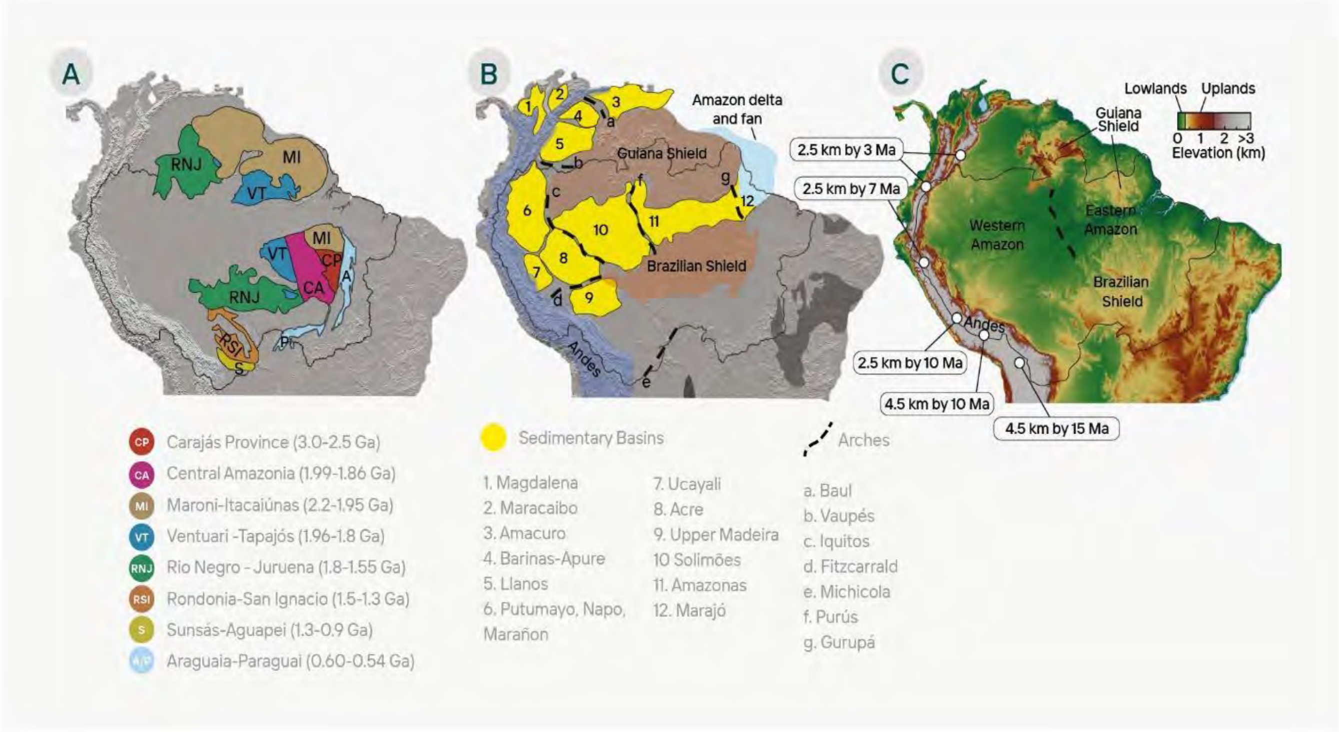


Figure 1.2 (A). Geochronological map of northern South America with the main provinces of the Amazon Craton (modified from Macambira *et al.* 2020). The area enclosing the known extent of late Meso- to early Neoproterozoic basement in the Northern Andes (fringing terranes). (B) Main foreland and intracratonic sedimentary basins of the Amazon (after Albert *et al.* 2018)**.** The location of the north Andean foreland basins is highlighted. (C) Elevation map for the Amazon, with prominent highlands in the eastern Amazon standing out in red/yellow colors. The Andes uplift ages indicated are based on published literature (Mora *et al.* 2008; Garzione *et al.* 2017; Sundell *et al.* 2019).

braided with some coastal sediments that accumulated in an intracontinental sedimentary basin that extended over parts of the Columbia supercontinent.

The Columbia supercontinent fragmented at c. 1.9 Ga (Zhao *et al.* 2004), but no fragmentation was recorded at the proto-Amazon Craton. An attempted breakup resulted in the Large Igneous Uatumã Province, a widespread phase of granite magmatism along the craton. The assembly of the Rodinia supercontinent (c. 1.2–1.0 Ga) marked the end and final stabilization of the Amazon Craton with the accretion of the Rondoniano-San Ignacio and Sunsás provinces to the current western margin of the Amazon Craton. It was during this new tectonic cycle that the Amazon Craton assumed the configuration that we know today, behaving from then onwards as a single tectonic entity (Figure 1.2.A). Much later, during the assemblage of the Gondwana supercontinent at the end of the Neoproterozoic (c. 640 Ma), the Paraguai and Araguaia fold belts were amalgamated to the southeast and south portions of the Amazon Craton.

1.2.2 Building the Lowland Rock Substrate: Sedimentary Basins

1.2.2.1 Amazonian Sedimentary Basins

After the breakup of Rodinia (c. 1.0 Ga) the Amazon Craton was embedded within the Gondwana supercontinent. At the beginning of the Paleozoic Era, an east-west rift developed across the middle of the Amazon Craton, almost splitting it into northern and southern portions (Wanderley-Filho *et al.* 2010). However, that rifting process did not persist, but instead resulted in the formation of an intracontinental depression that subdivided the craton into cores of what would become the modern Guiana and Brazilian Shields (Figure. 1.2). This depression formed the basement of the Solimões and Amazonas sedimentary basins. These E-W extending sedimentary basins in the middle of the Amazon Craton played a crucial role in forming present-day Amazonian landscapes. Over the past 400 million years, it was mostly a depression forming a seaway between the peripheral oceans and interior seas (e.g., the Paleomap Project by C. Scotese; www.scotese. com). This intracratonic depress-ion now also forms the pathway of the Amazon River, with its tributaries in the surrounding uplands.

1.2.3 Setting the stage: Pangea breakup and birth of the Andes

The tectonic separation of South America and Africa led to the opening of the South and Equatorial Atlantic Ocean. This separation and the eventual uplift of the Andes along the western margin of South America fundamentally altered the geological, geomorphological, and climatic conditions of the entire continent, and led to the current geographic configuration (Figure. 1.3 and Fig. 1.4). The breakup of Pangea eventually transformed this supercontinent into multiple smaller continents, including South America, Africa, and the Indian subcontinent, with Antarctica and Australia breaking away from South America around 45 Ma (Seton *et al.* 2012). This paleogeographic rearrangement created new continental margins and large-scale drainage readjustments.

1.2.3.1 Creating an oceanic outlet for the proto-Amazon River (c. 100 Ma)

The timing of onset and paleogeography of the Amazon River is a matter of much debate. Caputo and Soares (2016) proposed that during the Cretaceous the main direction of river flow was westward, away from the Atlantic margin and through the intracratonic Amazon and Solimões basins. During this time the western margin underwent both passive and active margin phases, and had little topographic expressions except for isolated volcanoes (Ramos 2009; Martinod *et al.* 2020). Instead, Figueiredo *et al.* (2009) propose that the incipient Amazon River started flowing eastward soon after the initiation of the Equatorial Atlantic Ocean (c. 100 Ma). According to this hypothesis, during the Late Cretaceous (and after 100 Ma) the drainage system in Amazon was split into two basins. One basin was inherited from Pangea times, and continued flowing towards the west into the Pacific Ocean. The other newly-formed drainage basin flowed eastwards, draining the eastern Amazon and delivering cratonic sediments to the newly opened Equatorial Atlantic Ocean. The divide between the two basins would have been an elevated area conditioned by the tectonic complexity of the basement underneath, i.e., the Amazon Craton. This hypothesis is supported by the absence of Andean river sediments in the Atlantic Ocean until c. 10 Ma (Figueiredo *et al.* 2009; Hoorn *et al.* 2017), and by the progressive subsidence of the broken-up plate margin (McKenzie 1978). By this time, the paleo-Amazon drainage system was well developed in the eastern Amazon with an outlet in the Atlantic Ocean. To form its current transcontinental configuration, it needed to overcome a continental divide and connect with the western Amazon.

However, this connection could not form until (i) the paleo-Amazon river could erode its westernmost headwaters and (ii) rivers could bypass the western Amazon. These necessary pieces of the puzzle fell into place when the Andes became an ~4 km-high mountain range and the Subandean foreland tilted eastwards (Dobson *et al.* 2001; Figueiredo *et al.* 2009; Shephard *et al.* 2010; Hoorn *et al.* 2010b; Sacek 2014).

1.2.3.2 Westward drift of South America and Andes formation: Forging the Amazon's westernmost boundary and eastward tilt

The uplift of the Andes was fundamental to the formation of the Amazon we see today, with all the physiographic and climatic ingredients necessary to build its geologic and biologic diversity. Below we explain how the Andes formed.

As South America drifted westward during the opening of the Atlantic Ocean, the western margin of the South American plate experienced tectonic plate convergence, the driving force of mountain building. However, South America had no significant mountains along its west coast during most of the last 100 Ma. Despite the long history of westward drift and tectonic convergence on its western edge, it wasn't until the last 40 ± 10 Ma that the significant topographic expressions of the Andes began forming (Capitanio *et al.* 2011; Garzione *et al.* 2017). This delayed mountain building is puzzling and remains a matter of debate (e.g., Faccenna *et al.* 2017; Chen *et al.* 2019).

The Andes rose as high as 4 km in southern Peru by 10–15 Ma (Sundell *et al.* 2019). As uplift continued, the Andes also became wider, and by 7 Ma it reached 4–5 km elevation about 450 km away from Pacific Coast in southern Peru and northern Bolivia (Garzione *et al.* 2017). The southern Peruvian Andes became wider, while northern Peru, Ecuador, and Colombia had much less expressive topography (Figure 1.2.C).

Evidence diverges on paleoelevations during the Miocene, but it seems that it was not until 4–5 Ma that a 3 km high Andes flanked the Amazon's northwest (Mora *et al.* 2008). Importantly, when the Andes north of the Altiplano reached 2.5 km or more, atmospheric circulation was incrementally blocked, driving high orographic rainfall in the Andean foothills and fundamentally changing the climatic regime over South America (see Chapters 5 and 7). The Andean foothills got wetter, and parts of the eastern Amazon became drier (Ehlers and Poulsen 2009).

In the last 20 Ma, the rise of the Andes deformed the crust underneath the western Amazon, creating a large bowl-shaped terrain over which widespread wetlands could form, with occasional marine incursions (Hoorn *et al.* 2010b; Sacek 2014; See Section 1.3.2). Large sedimentary loads were exported from the uplifting and eroding Andes into the alluvial megafans, hinterland, and foreland basins (Wilkinson *et al.* 2010; Horton 2018). These processes also created the necessary conditions (i.e., thick and porous medium) to form the major groundwater aquifers (See section 1.6.3) in the region.

Mountain building, and the overfilling of wetlands by the large sediment loads, strongly controlled changes in the river network by pushing rivers further east. Together with the uplift of a lowland swell (i.e., Vaupés Arch), this was sufficient to interrupt the Orinoco River, formerly connected to the lowland western Amazon as far south as southern Peru, and a continent-wide river network began forming (Mora *et al.* 2010). At the same time, the paleo-Amazon River system in the eastern Amazon was growing westward by headwater erosion as suggested by Figueiredo *et al.* (2009). With the Andes continuously filling sedimentary basins in the western Amazon, the river network began bypassing the western lowlands, which flexed the litho-

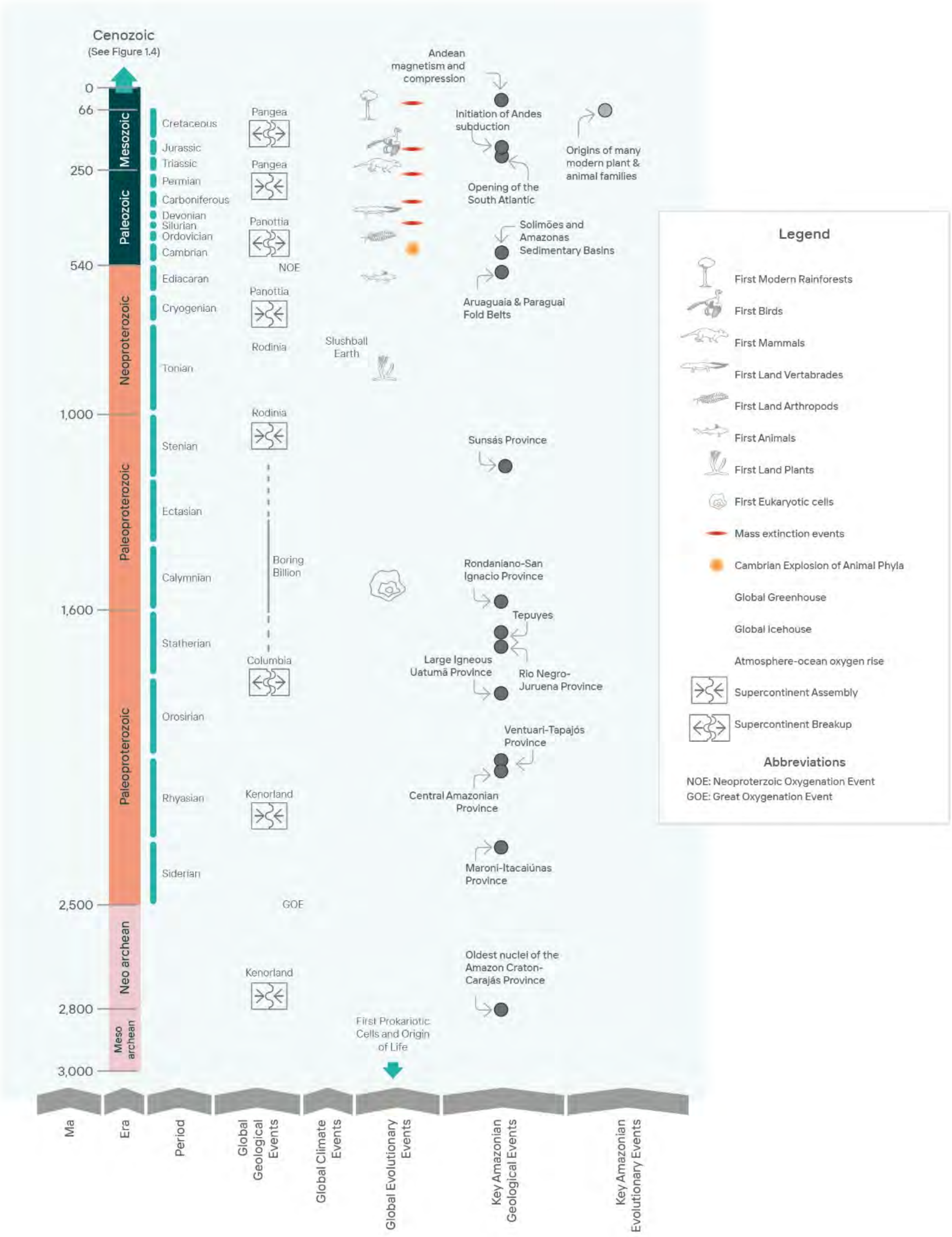


Figure 1.3 Geological time scale with the key global and Amazonian geological, climate and evolutionary events across time.

sphere under the western Amazon and began forming an eastward tilt (Sacek 2014). Largely disconnected from the Orinoco system and potentially with an added push from the mantle underneath South America, the western and eastern Amazonian river systems connected and began draining eastward towards the Atlantic Ocean (Figueiredo *et al.* 2009; Shephard *et al.* 2010; Hoorn *et al.* 2010b; Eakin *et al.* 2014; Sacek 2014) (see Section 1.3).

1.3 Towards the Modern Landscape

1.3.1 Past environments that left their imprint on the modern Amazonian landscape

1.3.1.1 Transition from fluvial landscape to large wetland

Formation of the Andes dramatically reshaped the geography of northern South America in the Neogene (Garzione et al. 2008, 2017), with the marine seaway along the western margin of the Amazon gradually drying up, transitioning to deltaic and lacustrine settings (Hoorn et al. 2010b) (c. 66–23 Ma; Figure 1.4.D.a-b). From c. 23 to 10 Ma much of the western Amazon was covered by an immense mega-wetland known as the Pebas System (Wesselingh et al. 2001, 2006; Hoorn et al. 2010a, b) (Figure 1.4.D.c). This shallow, lake-dominated wetland system extended over c. 1 million km2, at a maximum reaching about 1,500 km E-W from the Andean foothills to the easternmost limit of the western Amazon near Manaus, Brazil. These wetlands also extended 1,200 km N-S along the Subandean foreland from the modern Ucayali River in Peru to the modern Caquetá River in southern Colombia (Figure 1.4.C.c). Associated with the Andean uplift, plate mantle/interaction, and global (eustatic) sea level high stands, the western Amazon faced subsidence (downwarping) and uplift of structural arches (*e.g.,* Fitzcarrald, Iquitos, Vaupés; see Figure 1.2.B), which formed the margins of sedimentary basins in the western Amazon today (Espurt et al. 2007; Shephard et al. 2010; Eakin et al. 2014; Sacek 2014; Jaramillo et al. 2017; Bicudo et al. 2019, 2020).

The sedimentary record of the Pebas mega-wetland system is archived in the Subandean sedimentary basins of Colombia, Ecuador, and Peru, and in the Solimões, Acre, and westernmost part of the Amazonas sedimentary basins of Brazil (Wesselingh *et al.* 2001; Mapes 2009; Hoorn *et al.* 2010a, b) (Figure 1.2.B). Pronounced subsidence along the Subandes and in the western Amazon also facilitated marine incursions into the region (Hoorn 1993; Hovikoski *et al.* 2010; Hoorn *et al.* 2010a, b; Jaramillo *et al.* 2017).

The extent of marine influence is debated (Latrubesse *et al.* 2010; Gross and Piller 2020), but evidence is mounting that the Pebas wetland at times formed an estuarine embayment with tidal influence in the Llanos basin (Hovikoski *et al.* 2010; Boonstra *et al.* 2015; Jaramillo *et al.* 2017). The sedimentary units that represent the Pebas wetland are collectively called the Pebas, Curaray, or Solimões Formation, in Peru, Ecuador, and Brazil respectively. In Peru, their nutrient-rich surface and associated soils harbor a diverse and endemic-rich biota (Hoorn *et al.* 2010b; Higgins *et al.* 2011; Tuomisto *et al.* 2019).

The Pebas System was characterized by shallow, lake-dominated environments that deposited fine-grained sediments under frequently hypoxic (low oxygen) conditions.

Such a system could form and maintain itself for over 10 millions years because subsidence and sediment input were kept in pace with one another (Wesselingh *et al.* 2001; Hoorn *et al.* 2010a, b). Most remarkable is the rich endemic fauna of mollusks and reptiles that inhabited its shores, but which went extinct after the disappearance of this environment (Wesselingh *et al.* 2006, Riff *et al.* 2010) (see chapter 2). The system was at its maximum extent during the Middle Miocene Climatic Optimum, from c. 17–15 Ma, coinciding with global sea level highstand (Miller *et al.* 2020; Westerhold *et al.* 2020; Methner *et al.* 2020) (Figure 1.4).

1.3.1.2 From Wetland to Amazon River and Megafans

By c. 10 Ma, the Pebas wetland system transitioned into alluvial megafans and the Acre fluvial system (Hoorn *et al.* 2010a, b). This change in sedimentary regime was caused by increased erosion and sediment output, possibly due to accelerated Andean uplift, and climate change from the late Miocene onwards (Figure 1.4.; Harris and Mix 2002). Together, these processes had a transcontinental effect, stretching from the Andes to the deep-sea fan system on the Atlantic margin. Evidence for this can be found both in the Subandean basins (e.g., Parra *et al.* 2009) and at mouth of the Amazon River (*Foz do Amazonas*) (Figure 1.4.D.d,e). The latter has a sedimentary record that displays a clear change in sediment geochemistry, from cratonic to Andean sediment at c. 10 Ma (Figueiredo *et al.* 2009; Hoorn *et al.* 2017; van Soelen *et al.* 2017).

Other models propose a Pliocene (c. 4.5 Ma; Latrubesse *et al.* 2010; Ribas *et al.* 2012) or even Pleistocene (<2.6 Ma; Rossetti *et al.* 2015) age for the onset of the transcontinental Amazon River. Empirical data on the ages of *terra firme* surfaces along the Amazon River in the western Amazon show maximum ages of 250 ka (Pupim *et al.* 2019) suggesting that the most recent surfaces are relatively young (geologically speaking). Perhaps these different interpretations arise in part due to alternative definitions of the Amazon River, different dating methods, the longevity of geomorphic features, and data types used by different studies (see review in Albert *et al.* 2018).

1.3.1.3 Quaternary Climate and Landscape Changes in the Amazon

The Quaternary covers c. 2.6 million years of history, during which the climate across the globe and in the Amazon drastically changed because of the onset of glacial-interglacial fluctuations (Lisiecki and Raymo 2005, 2007) (see Box 1.2). The climate dynamics of the Quaternary also substantially affected biotic and abiotic (e.g., megafans, sedimentary deposits) landscapes of the Amazon (Cheng *et al.* 2013; Baker and Fritz 2015; Govin *et al.* 2014, Hoorn *et al.* 2017) (Figure 1.4.D.f).

In terms of precipitation, the Amazonian hydrological cycle is closely tied to the seasonal movements of the intertropical convergence zone (ITCZ) over the Atlantic, which shapes the South American monsoon (e.g., Garreaud *et al.* 2009, Novello *et al.* 2019). Additional precipitation forcing is caused by substantial rainforest transpiration playing a role in the onset of the monsoon (Wright *et al.* 2017) and contributing large amounts of water vapor and precipitation to the Amazon drainage basin (Langenbrunner *et al.* 2019). The dry-to-wet transition season is additionally influenced by the significant amount of evapotranspiration from the Amazonian forest canopy landscape (Wright *et al.* 2017).

Quaternary climate changes affected both the intensity and mean latitude of the ITCZ, atmospheric convective systems, and the trade winds. Precipitation regimes over South America changed substantially following shifts in the intensity of the South American monsoon, the South American

Box 1.2 Pleistocene Climate and Sea Level Fluctuations

Global climate fluctuations during the Pleistocene (c. 2.6–0.01 Ma) have driven multiple cycles of eustatic (or worldwide) sea level changes, with several of the most recent cycles exceeding 100 m vertical change from minimum to maximum sea stands. During warm interglacial periods, elevated sea levels slowed river discharges to the sea, allowing sediments to settle out and build up floodplains. During cool glacial periods, lowered sea levels allowed rivers to incise more deeply into their sediment beds as they approached their mouths, eroding floodplains and steepening the river gradient. This repeated formation and erosion of Amazonian whitewater floodplains (i.e., *várzeas*) during sea level high and low stands is referred to as the Irion Cycle (Irion and Kalliola 2010).

Erosion during sea level low stands excavated the lower portions of rivers in the eastern Amazon, forming deep ría lakes near the mouths of large clearwater rivers like the Tocantins, Xingu, and Tapajós. Sea level rise after the LGM allowed sediments to fill the canyon that had formed in the lower portion of the Amazon-Solimões River, so that the bed of the modern Amazon is 10–50 m higher than that of the ria lakes of its adjacent tributaries. By lowering the topographic base-line for erosion, low sea levels also induced the formation of waterfalls and rapids in these upstream tributaries.

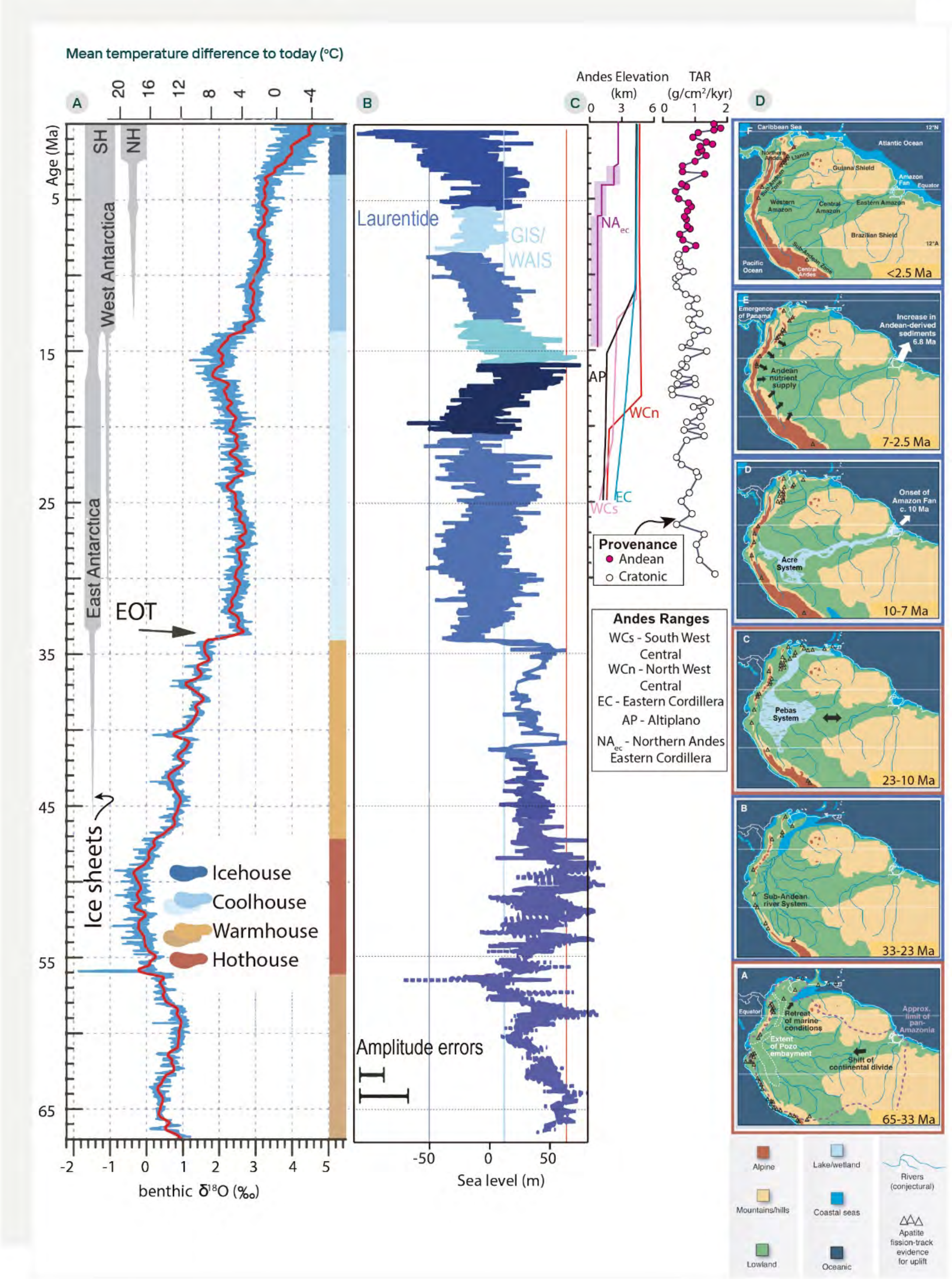


Figure 1.4 A) Global Cenozoic temperature curve (from Westerhold *et al.* 2020); B) Global Cenozoic sea level curve (from Miller *et al.* 2020) (see Box 1.2); C) Past elevation estimates for the Central Andes (after Sundell *et al.* 2019), and temporal variations in εNd in the Amazon submarine fan (red, after Figueiredo *et al.* 2009; Hoorn *et al.* 2017), Ceará Rise (black, after van Soelen *et al.* 2017) and Terrigenous Accumulation Rates (TAR) at the Amazon outlet near the Ceará Rise; D) Paleogeographic maps illustrating the transition from Amazon Craton to Andes-dominated landscapes: (a) The Amazon once extended over most of northern South America. Breakup of the Pacific plates changed the geography and the Andes started uplifting. (b) The Andes continued to rise with the main drainage toward the northwest. (c) Mountain building in the Central and Northern Andes (~30 Ma, specially from 12 Ma) and wetland progradation into the western Amazon. The Middle Miocene Climate Optimum and high sea level caused marine ingressions and estuarine conditions in the heart of the Amazon. (d) Uplift of the Northern Andes restricted "pan-Amazonia" and facilitated allopatric speciation and extirpation [e.g., (21)]. (e) The mega-wetland disappeared and *terra firme* rainforests expanded; closing of the Panama Isthmus and start of the Great American Biotic Interchange (GABI). (f) Quaternary. Note that South America migrated northward during the course of the Paleogene.

low-level jet, the Bolivian high, and the South Atlantic Convergence Zone (see Chapters 5 and 7). Our knowledge of precipitation patterns during the Quaternary is based on scattered archives from ice cores and lakes in the Andes, marine records from the Brazilian coast, and caves throughout the Amazon. The latest assessments hint at the complex history of shifting patterns of hydrological variation throughout the region (e.g., Thompson 1998; Sylvestre 2009; Govin *et al. 2014*; Novello *et al.* 2017, 2019; Hoorn *et al.* 2017; Wang *et al.* 2017).

Evidence from paleorecords that cover the last two glacial-interglacial cycles (c. 250,000 years) reveals distinct climate profiles in the eastern and western Amazon, the so-called South American precipitation dipole (Cheng *et al.* 2013). This dipole consists of a differential precipitation pattern over the Amazon, where wet-dry conditions varied substantially in the eastern Amazon, while precipitation variability was much less in the western Amazon, including the Andes (Cheng *et al.* 2013; Baker and Fritz 2015, Wang *et al.* 2017). The effect of this precipitation dipole on biotic landscapes is poorly known, as fossil pollen sequences in the lowland Amazon often lack time series older than 50,000 yr (Flantua *et al.* 2015). However, records covering the last glacial period around c. 21 ka show different species composition and structures of lowland and Andean forests when compared to the present (Mayle *et al.* 2009), without necessarily a shift between biomes (Häggi *et al.* 2017). Paleo-records from the highlands, including glacier snowline reconstructions and fossil pollen records (e.g., Flantua *et al.* 2014, 2019), also indicate the persistent influence of Quaternary climate fluctuations on the Andean Amazon. Temperature ranges over a full glacial-interglacial cycle differed across the Amazon; current estimates are 2–5°C for the Amazonian lowlands and 5–10°C in the high Andes (above 2,500 m) (e.g., Klein *et al.* 1995; Mayle *et al.* 2004; Mark *et al.* 2005; Groot *et al.* 2011; Hooghiemstra and Flantua, 2019). Although temperatures were equally low during glacial periods in the northern Andes, they were substantially drier than in the central Andes (Torres *et al.* 2013), creating an additional precipitation dipole of paleoclimate within Amazonia but across the Andes. Cool temperatures during glacial periods were accompanied by large changes in moisture availability linked to the South American monsoon system, causing substantial advances of glaciers across the Andes (Palacios *et al.* 2020).

The waxing and waning of glacial-inter-glacial-cycles influenced Amazonian landscapes in many ways. The combination of global climate cooling during the Pliocene-Pleistocene (last 4 Ma) and the alterations of glacial processes are presumed to have increased glacial erosion globally (Herman *et al.* 2013). Increased precipitation accelerated erosion and sediment transport during interglacial periods, while extensive moraines paved valleys to elevations as low as 2,500 m (Angel *et al.* 2017; Mark *et al.* 2005). Erosion rates may have been highest during transitions to and from glaciated to ice-free conditions (Herman and Champagnac 2016), and sediment flux was disproportionately high during the high-amplitude climate oscillations of the last one million years (Robl *et al.* 2020). High denudation of the Andes during the Quaternary contributed to the formation of megafan alluvial piles in portions of the sub-Andean foreland (Wilkinson *et al.* 2010).

1.3.2 Modern landscapes in the Amazon

As reviewed in Section 1.3.1, modern landscape geo-diversity from the continental scale down to river margin terraces is a cumulative function of tectonic, geomorphological, and climatic processes operating over millions of years.
Amazonian landscapes can be classified by the main features of their geologic settings, which affect all surface features from soils and rivers to species and ecosystems. Importantly, almost everything we know about the history of Amazonian landscapes comes from materials preserved in the geological record.

Landscape morphology is a description of the spatial distribution of elevations, resulting from the balance between uplift, erosion, and deposition. Thus, terrain steepness and sediment loads in rivers reflect how fast an area is uplifting (e.g., Hack 1960; Ahnert 1970; Milliman and Syvitski 1992; Montgomery and Brandon 2002; Portenga and Bierman 2011).

Tectonic compression uplifts mountain ranges in the Andes, while rivers remove all or part of that uplift just as fast, producing sediments and nutrients which are then transported downriver (e.g., Wittmann *et al.* 2011; Garzione *et al.* 2017). Thus, the Andes mountains have local amplitudes of elevation (i.e., range of elevation in a given radius, henceforth referred to as *relief*) upwards of 3 km within a 2.5 km window. These high relief areas are a testament to the forces driving uplift and produce high erosion rates (c. 100–1,000 m/Ma) at the westernmost edges of the Amazon, yielding 300–600 Mt/yr in the Lower Solimões River (Wittmann *et al.* 2011). These high sediment loads come from nutrient-rich areas within the Amazon drainage basin (see Section 1.4), which sets the stage for different types of aquatic and floodplain habitats (see Section 1.5). Importantly, these mountains block atmospheric currents and produce steep local climatic gradients, called orographic effects, focusing meters of rain on the eastern slopes of the Amazonian Andes (Bookhagen and Strecker 2008). Together, the high relief and sediment yield of the Andes and its local effects on climate and vegetation have been identified as key ingredients in generating and maintaining biodiversity (Antonelli *et al.* 2018).

In contrast, the lowland landscapes of the western and eastern Amazon have low relief (<200 m), mainly because of low uplift rates. Mostly, rivers flow over easily erodible sedimentary rocks from the sedimentary basins that form the substrate for most of the western and eastern Amazonian lowlands. Although the low relief and mostly uniform topography of the interfluves suggest these landscapes are at equilibrium with local uplift rates, the western Amazon lowlands are highly dynamic. Here, the low slopes pave the way for highly energetic and dynamic meandering rivers (i.e., Beni, Mamoré, Juruá, Purús, Madeira, Solimões), which migrate back and forth over their floodplains at rates from 10 m/year to >100 m/year, carving curved floodplain walls and even avulsing into new valleys (e.g., Mertes *et al.* 1996; Gautier *et al.* 2007). Compiled geochronologic data along the Amazon whitewater floodplain suggest that active floodplain deposits are at most 20 ka (Pupim *et al.* 2019), placing a limit on the time for river channels to sweep across the active floodplain. *Paleovárzeas* above the active floodplains are also preserved in some places (e.g., Lago Amanã), persisting through more than one glacial cycle of erosion and deposition of floodplain sediments (Irion and Kalliola 2010). These complex hydrogeomorphic dynamics generate high spatiotemporal heterogeneity on Amazonian lowlands, contributing to, for instance, exceptionally high local fish diversity (Saint-Paul *et al.* 2000; Correa *et al.* 2008; Goulding *et al.* 2019).

In contrast to the lowlands of the western Amazon, the eastern Amazon's lowland rivers flow mostly over the Alter-do-Chão Formation (moderately re-

Box 1.2 Pleistocene Climate and Sea Level Fluctuations

Global climate fluctuations during the Pleistocene (c. 2.6–0.01 Ma) have driven multiple cycles of eustatic (or worldwide) sea level changes, with several of the most recent cycles exceeding 100 m vertical change from minimum to maximum sea stands. During warm interglacial periods, elevated sea levels slowed river discharges to the sea, allowing sediments to settle out and build up floodplains. During cool glacial periods, lowered sea levels allowed rivers to incise more deeply into their sediment beds as they approached their mouths, eroding floodplains and steepening the river gradient. This repeated formation and erosion of Amazonian whitewater floodplains (i.e., *várzeas*) during sea level high and low stands is referred to as the Irion Cycle (Irion and Kalliola 2010).

Erosion during sea level low stands excavated the lower portions of rivers in the eastern Amazon, forming deep **ría lakes** near the mouths of large clearwater rivers like the Tocantins, Xingu, and Tapajós. Sea level rise after the LGM allowed sediments to fill the canyon that had formed in the lower portion of the Amazon-Solimões River, so that the bed of the modern Amazon is 10–50 m higher than that of the ria lakes of its adjacent tributaries. By lowering the topographic base-line for erosion, low sea levels also induced the formation of waterfalls and rapids in these upstream tributaries.

sistant siltstones and sandstones). Here, rivers are also low-relief (10–200 m), except for where resistant sandstones outcrop in the Pará state (Brazil), where local relief can reach 400+ m. Despite having a relatively uniform relief distribution which could indicate equilibrium landscapes, northern and southern tributaries to the Amazon River between the confluence of the Rio Negro and Solimões River are riddled with rapids and waterfalls, especially near the limits between the lowlands and uplands (i.e., João *et al.* 2013; Val *et al.* 2014; Val 2016). Also, the long-term stability of the Amazon River margins has allowed for the development of lateritic crusts (e.g Balan *et al.* 2005; Horbe and da Costa 2005), which are locally faulted (Silva *et al.* 2007). Together with evidence of fluvial incision and paleochannel features and deposits (e.g., Hayakawa *et al.* 2010), these landscapes are likely not equilibrated, which has led authors to argue for intracontinental faulting and glacio-eustatic sea level change as triggers of landscape change (Irion and Kalliola 2010; Val *et al.* 2014; Rossetti *et al.* 2015). Although these are all plausible interpretations, the true origin of knickpoints (waterfalls and rapids) in the eastern Amazon is not currently known but may be key to constraining the timing of landscape changes where river deposits are absent.

Where rivers flow over and out of cratonic areas (i.e., shields), spatial changes in relief are drastic and likely long-lasting. Extending over all the northern and southern edges of the Amazon's drainage basin, there are outcrops of cratonic rocks, which form wide plateaus mostly with 500 – 1,000 m elevation but reaching upwards to 2,500 m in the northernmost reaches of the Amazon in southern Venezuela and at the border between Brazil and Guyana (Figure 1.2.c). Here, the so-called *Tepui* form astounding table-top mountains which are supported by highly-resistant metamorphic rocks of the Amazon Craton and stand tall above the Amazon lowlands (e.g., Briceño and Schubert 1990; Rull *et al.* 2019, see Section 1.2). This is where the deep-time geologic evolution of the Amazon manifests itself on the current landscape the most. Whether these plateaus are uplifting, and if so, how fast, is unknown, but likely on orders of magnitude lower than in the Andes. Nonetheless, local flexural uplift due to the weight of the sedimentary and igneous (i.e., sills) piles in the Amazon sedimentary basin as well as in the deep-sea fan could contribute to maintaining some of these plateaus (Nunn and Aires 1988; Watts *et al.* 2009). These highly resistant, more than a billion-year-old rocks impede erosion and landscape lowering. Lateritic duricrusts 5 to 60 Ma in age are still preserved in the eastern Guiana Shield, suggesting <5 m/Ma erosion rates (Théveniaut and Freyssinet 2002; Balan *et al.* 2005; dos Santos Albuquerque *et al.* 2020). On millennial timescales, the shield areas erode at 10–40 m/Ma and contribute 9–20 Mt/yr of sediments via the Negro and Tapajós rivers (Wittmann *et al.* 2011). So far, erosion rates are scarce but highly important to determine how fast upland areas were integrated with the lowland basins through the geologic past. This is an important gap in knowledge as these plateaus harbor many range-restricted and endemic species (Albert *et al.* 2011; Cracraft *et al.* 2020; see also chapter 2).

In summary, the geological contrasts described above are 1) deeply entrenched rivers in the uplifting Andes with a mix of equilibrium and non-equilibrium landscapes; 2) low-relief, near-equilibrium landscapes in the western Amazon lowlands over relatively soft sedimentary rocks with textbook examples of dendritic and meandering fluvial patterns; 3) complex topographic forms in the shields with low-relief plateaus surrounded by intensified river excavations and anomalous river network configurations due to lithological contrasts. Importantly, low-relief drainage divides exist in many portions at the edges of the Amazon River, such as its divide with the Orinoco, Essequibo, and Paraná-Paraguay-Uruguay river basins, and indicate that the Amazon River basin is still undergoing transience (e.g., Albert *et al.* 2018; Stokes *et al.* 2018). Despite the absence of known active tectonic uplift, central and eastern Amazonian landscapes are prone to autogenic processes, and also to external base level perturbations that can ultimately lead to river network changes. These processes are 1) dynamic topography, 2) glacial-interglacial base level fluctuations (Box 1.2), 3) river capture (Box 1.3), and 4) river avulsions (Box 1.3). Lastly, erosion rates are largely unconstrained in the Amazon and only restricted to the largest tributaries (Wittmann *et al.* 2011). There is essentially no published long-term erosion rate data in the lowland Amazon and very few rates are available for the shield areas and for the Andes mountains. These are major data gaps. Constraining background sediment production will not only allow for constraining deeper links between landscape and species evolution. It is also of major importance to assess the impacts of anthropogenic activities such as agriculture as well as the effects of deforestation and wildfires on sediment yield and habitat degradation in a future of climate change.

1.4 Richness of the Amazonian Landscape: Geodiversity and Soils

Soils form at the interface between geology, biology, and hydrology, constitute an integral part of the physical environment for continental ecosystems, and serve four main ecological functions. Soils facilitate (i) the storage, supply, and purification of water; (ii) plant growth; (iii) atmospheric modifications; and (iv) habitats for organisms and microorganisms. Moreover, soils provide essential resources for primary production (i.e., photosynthesis) through the availability of essential mineral elements and water that support terrestrial and aquatic food webs. Soil transformations through time, therefore, control nutrient availability and profoundly influence the water chemistry in both terrestrial and aquatic ecosystems. The evolution, diversity, and geographic distribution of soil types affect all continental ecosystem functions. Here, we review aspects of the interaction between geological processes, time, and soil evolution in the Amazon, and how this regional geodiversity contributes to ecosystem functions.

1.4.1 Geodiversity has shaped Amazonian soils

Geological processes, such as those described in sections 1.2 and 1.3, have shaped the geographic

Box 1.3 Drainage modification through river capture and avulsion

River capture, sometimes referred to as stream piracy, is the process by which the tributaries of one river basin capture a fraction of a neighboring river network. River captures often arise from an imbalance in erosion rates between streams sharing a drainage divide. The transfer of tributaries among river basins moves the position of the drainage divide, and is often recognizable by abrupt changes in the thalweg or valley-line of river courses, such as characteristic hair-pin or U-shaped turns. In regions with rocky substrates, river capture results in the formation of narrow gorges or wind gaps, as well as topographic discontinuities represented as knickpoints in the longitudinal river profile. Such knickpoints are often the location of rapids or waterfalls, which are propagated upstream by progressive erosion. The upstream movement of knickpoints is a universal consequence of base level fall, stripping the landscape of its uppermost soil mantles. Base level fall resulting from river capture or lowered sea level is an understudied mechanism of landscape change in the Amazon, but likely to have been very important. Depending on several variables, landscape transience can persist for millions of years in the tectonically stable shield landscapes. Important variables driving river capture and watershed migration include the elevational magnitude of base level falls, differences in basin sizes on either side of a watershed divide, differences in precipitation and lithology on either side of a watershed divide, and the ensuing slope-driven stream erosion power.

River avulsions are changes in the position of active river channels that arise from hydrological and geomorphological processes. Avulsions are usually autogenic in nature and span timescales of years to thousands of years (Slingerland and Smith 2004). As rivers avulse into another channel, they leave fluvial “scars” behind, also called fluvial escarpments, as well as alluvial fans, which are kilometer-wide fan-shaped sedimentary deposits. Fluvial escarpments are widespread in the lowland Amazon and indicate that hundreds of kilometers of river avulsion are an intrinsic part of the lowland alluvial rivers, with important implications for biogeography and biodiversity (Albert *et al.* 2018; Tuomisto *et al.* 2019). The largest avulsions form alluvial megafans, and are also widespread in Amazon with variable ages since the late Miocene (Wilkinson *et al.* 2010).

distribution and physiographic coverage of edaphic conditions in the modern Amazon. Soil formation and evolution occur through the interactions of five major factors (Jenny 1941): parent material (e.g., rock type and minerals), geomorphology (local landscape relief), climate (hydrological and evaporative regimes governing water fluxes through sediments), interactions with organisms (e.g., soil and root-associated microfauna and meiofauna), and time. These factors act together to create the conditions where a given type of soil occurs. Soils are dynamic formations that reflect the inputs of many contributing abiotic (lithological, hydrological, climatic) and biotic factors, including chemical and physical modifications by bacteria, mycorrhiza, plants (e.g., roots, leaf litter) and animals (e.g., meiofauna, earthworms, arthropods).

Time changes both the morphological and chemical characteristics of soils in predictable ways. At the beginning of the soil forming process the flat surface develops a thin layer of unconsolidated material over the rock through the physical effect of climate (e.g., variations in temperature and moisture) and the pressure exerted by plant roots. Over thousands to millions of years, the soil will deepen and the effects of weathering (see section 1.4.2) will transform the structure of the soil minerals and their chemistry until a more stable, nutrient poor, and deeper soil is formed. Mature soils are resistant to further changes in the absence of pronounced landscape-scale transformations. If developed on a sloped surface, faster erosion might outpace the subsoil formation, keeping the soil young and shallow irrespective of how long it has been exposed. The continuous wet and warm climate and widespread presence of soil organisms across the Amazon imply that geological time, parent material, and geomorphology are the main factors controlling soil development. The influence of these factors, however, varies with spatial scale (Figure 1.5).

Interactions between geological and climatic factors across scales have produced a complex mosaic of soil types and conditions across the Amazon, each with distinct physical, chemical, and biological properties. At basin-wide scale, the processes described in sections 1.2 and 1.3 resulted in large differences in the age and erosion rates of parent material (i.e., time since the substrate was exposed to weathering), forming different geological provinces (Figure 1.2A) with variation in soil nutrient status (Figure 1.5).

About 60% of soils in the Amazon drainage basin are highly-weathered, nutrient-poor ferralsols and acrisols, concentrated mainly in the eastern Amazon (Quesada *et al.* 2011). The parent material of the Guiana and Brazilian shields is Proterozoic in age and highly weathered. Many shield soils developed over crystalline rocks instead of sedimentary rocks or unconsolidated sediments, which have very low erosion rates (Section 1.3.2). Their weathering occurs at a slower pace and many shield soils have a somewhat higher nutrient status when compared to the comparatively younger soils occurring east of the Negro-Solimões river confluence in the intracratonic basin. During filling of the Amazon's sedimentary basins, for example, Paleozoic-Mesozoic sediments originating from weathered Proterozoic rocks resulted in lower soil fertility (Quesada *et al.* 2010) (Figure 1.5. A and B).

By contrast, soils in the western Amazon generally are more nutrient-rich, as they formed in recent sediments that eroded from the Andes (Quesada *et al.* 2010, 2011; Quesada and Lloyd 2016). Much of the sediments deposited in the western Amazon during the Miocene were protected from weathering due to waterlogging during the Pebas megawetland phase (23–10 Ma, see Sections 1.2 and 3). Therefore, processes of soil formation in much of the western Amazon are significant only from the Pliocene (c. 5 Ma) onwards, with much of the region having soils that are less than 2 million years old (Quesada *et al.* 2011).

Although geological time and erosion rates explain basin-wide variations in soil development and fertility, variations in parent material and geomorphology are the main factors influencing local variations in soil type. Processes associated with geomorphology, such as topographic position (plateau, slope, and valley), drainage, and local erosion can influence soil formation strongly, resulting in different soils occurring at a scale of tens of meters, despite being formed on the same lithology (Catena Formation, Fritsch *et al.* 2007). The interaction of these factors results in an exceptionally high diversity of soils, with diverse physical and chemical properties. For example, at least 19 of the 32 World Reference Base (WRB) soil groups occur in the Amazon (Quesada *et al.* 2011), which only lacks soils associated with dry or cold environments.

1.4.2 Soil diversity influences ecosystem function and biodiversity

Soil development occurs because of physical and chemical weathering of parent rock and regolith, and nutrient enrichment from allochthonous sedimentary deposition and autochthonous organic decomposition. Chemical weathering processes (carbonation, dissolution, hydrolysis, oxidation-reduction) are accelerated in the hot and humid climates of lowland Amazonian rainforests, while physical weathering is more active in the high Andes. Physical weathering occurs through geomorphic processes that break soil particles into smaller sizes, whereas most chemical weathering of Amazonian soils involves reactions with water.

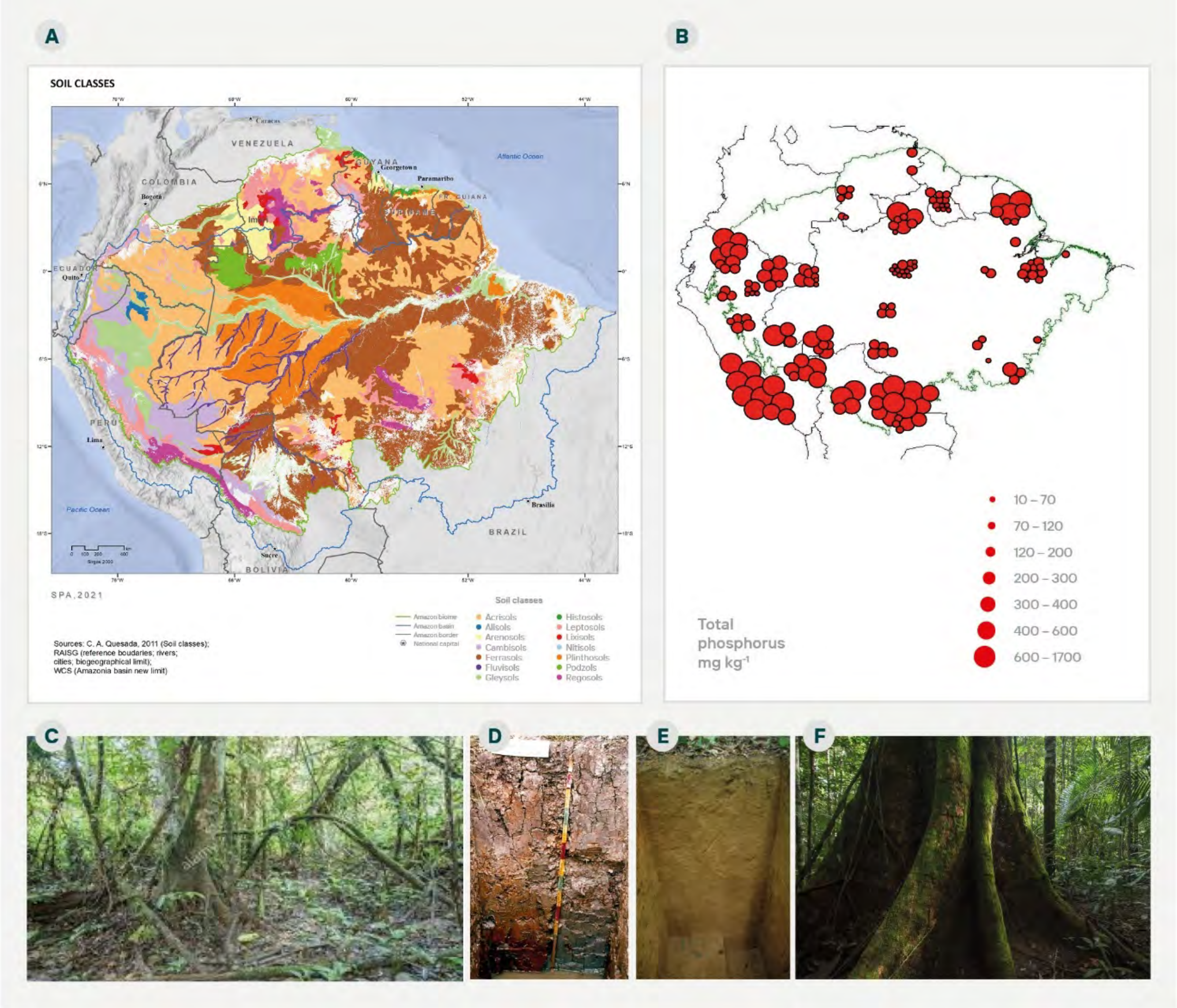
Weathering reduces the concentrations of many mineral elements essential for plant growth, such as phosphorus, calcium, magnesium, and potassium. Weathering also alters soil mineralogical composition and morphological characteristics (Quesada *et al.* 2010). This ultimately results in associations between major groups of soil classification and nutrient distribution (Figure 1.5.A). Soil phosphorus serves as an important indicator of soil development, as total phosphorus content decreases during soil weathering.

Because the phosphorus pool is gradually transformed to unavailable forms, phosphorus is the main nutrient limiting ecosystem productivity in ancient Amazonian soils (Quesada *et al.* 2012; Quesada and Lloyd 2016). On the other hand, nitrogen is mainly supplied to soils through atmospheric nitrogen deposition and microbial N_2 fixation, thus accumulating throughout soil development. Nitrogen is not limiting in mature forests, but nitrogen limitation does occur in disturbed forests (e.g., logging, fires, large scale mortality events) and white sand forests (Quesada and Lloyd 2016).

Forests are not solely affected by soils through nutrient availability. Younger soil types that have not suffered extensive weathering almost invariably show a lower degree of vertical development, often being shallow and with hard subsurface horizons that restrict root growth (Figure 1.5.C-D). Soil types that have resulted from many millions of years of weathering usually have favorable physical properties, such as well-developed soil structure, good drainage, and, due to their depth, high water storage capacity (Figure 1.5. E-F). This trade-off between physical quality and nutrient availability contributes strongly to the diversity of environments in the Amazon and causes deep effects on how the ecosystem functions.

Soil physical properties, such as shallow soil depth, poor drainage, and physical impediments to root growth, can be an important source of limitation to forest growth, directly or indirectly influencing tree mortality and turnover rates (Quesada and Lloyd 2016). Soil physical properties change patterns of above-ground vegetation biomass (Quesada *et al.* 2012), and how biomass is stored in individual trees (Martins *et al.* 2015). Physically constrained soils with high rates of tree mortality tend to be dominated by many small trees, while forests growing in favorable physical and low-disturbance soil conditions allow trees to live longer and accumulate more biomass. Soil physical properties are also related to the abundance of palms in the Amazon (Emilio *et al.* 2014), and to tree shape through their effects on the relationship between tree height and diameter (Feldpausch *et al.* 2011). Similarly, soil physical characteristics also influence forest demographic structure (Cintra *et al.* 2013) and dead wood stocks (Martins *et al.* 2015). On the other hand, forest growth rate (biomass production) is directly influenced by soil nutrient availability. Direct evidence of nutrient limitation on forest productivity has been reported by Quesada *et al.* (2012), which demonstrated that rates of biomass growth were correlated to variations in total soil phosphorus concentrations across the Amazon.

The importance of soils for tree species richness in the Amazon is controversial. Some studies report that species richness was generally negatively correlated with soil nutrient status, while others report a positive correlation (Faber-Langendoen and Gentry 1991; Phillips *et al.* 2003; Ruokolainen *et al.* 2007). In any case, tree species distributions are often associated with soil properties. Significant relationships between tree distribution and soil nutrient concentrations were found for at least a third of the tree species in the lowland forests of Colombia, Ecuador, and Panama (John *et al.* 2007). Higgins *et al.* (2011) show that floristic patterns in Amazonian forests were associated with soil variations across different geological formations, with this corresponding to a 15-fold change in soil fertility and an almost total change in plant species composition, suggesting that, to a large degree, floristic patterns may be related to underlying geological patterns (Quesada and Lloyd 2016).



Sources: C. A. Quesada, 2011 (Soil classes); RAISG (reference boudaries; rivers; cities; biogeographical limit); WCS (Amazonia basin new limit)

Figure 1.5 A) The complexity of soils across the Amazon; the majority are highly weathered, the rest varying from well-developed to young soil profiles. Parent material (geological substrate) and soils are directly related, but there is no relation with age of rocks. The E-W depression of the lower Amazon River has very poor soils; the crystalline rocks in the eastern Amazon are intermediate; the 'Andes-derived' substrates in the western Amazon have rich soils (Quesada *et al.* 2011). B) Phosphorus gradient in Amazonian soils, with a clear trend from phosphorus-rich soils in the west to phosphorus-poor soils in the east (Quesada and Lloyd 2016). C-D) Gleysols, non-weathered soil and biomass-poor soil in the western Amazon; E-F) Ferralsols, weathered soil and biomass-rich forest in the eastern Amazon (photo credits: B. Quesada, João Rosa).

1.5 Amazonian Hydrology: Rivers, Wetlands, Soil Waters, and Groundwaters

Water supports life directly, and indirectly modulates many processes essential to life. The varied distribution of water across the Amazon, at seasonal to geological time scales, provides the physiographic backdrop for both terrestrial and aquatic life. Below, we examine the modern-day Amazonian hydrological landscape as a product of geological and climatic gradients, and highlight the salient features relevant to understanding Amazonian biodiversity.

1.5.1 Geological and Climatic Diversity Shapes Hydrological Diversity across the Amazon

Under a given climate, topography, substrate, and vegetation cover, which could be even more important than geological substrates, control how much rainfall directly enters the surface drainage network (surface runoff), and how much infiltrates into the subsurface. While surface flow mobilizes sediments and nutrients into aquatic systems, the subsurface material stores the infiltrated water, promoting chemical weathering, and slowly releases water and solutes to streams as baseflow. Subsurface storage is also a source for root zone soil water for plants during rainless periods. Across the Amazon, substrate properties controlling this surface-subsurface partition (e.g., slope, permeability, and regolith or sediment thickness) vary dramatically. This creates a spatial mosaic in the landscape with hints on where water is shed or collected. Where there is substantial storage capacity in the subsurface (soils, regolith, fractured rocks), soils and rivers do not dry up quickly and ecosystems are more resilient to fast changing weather events and seasonal droughts (Hodnett *et al.* 1997; Cuartas 2008; Tomasella *et al.* 2008; Neu *et al.* 2011). Figure 1.6 illustrates the factors described above, which shape the hydrological plumbing of the system (cartoon in center).

The depth to the groundwater table (bottom map, Figure 1.6) is a good indicator of hydrologic conditions across the Amazon. Water table depth (WTD), ranging from zero (at land surface) to over 80 m (see color bar in Figure 1.6), reflects both the climate (vertical fluxes) and terrain (lateral fluxes above- and belowground). Shallow groundwater sustains streamflow and soil moisture in drought periods. Upland ecosystems over a deep water table are solely rainfed and vulnerable to meteorological droughts, whereas lowland ecosystems on shallow water tables, sustained by upland rain through downhill flow, enjoy a more stable water supply. Shallow WTD also causes waterlogging and anoxic soil conditions, excluding upland vegetation that is intolerant to waterlogging, and selecting wetland species well-adapted to waterlogging.

The spatial structure of WTD bears a strong signature of the topography, directly because surface slope controls drainage, and indirectly through its influence on climate (orography, lapse rate), regolith (weathering, erosion and deposition), and soil (substrate stability). These terrain features lay the physiographic foundation of diverse hydrologic features.

The strong climatic gradient across the Amazon, particularly in rainfall amount and seasonality, is another force shaping hydrologic diversity. The interaction of climate and topography results in a rich spatial-temporal pattern of water availability across the Amazon. However, except for the streamflow, hydrologic variables critical to ecosystems, such as root-zone soil moisture and WTD, are only sparsely observed across the vast Amazon, and here we use a model (Miguez-Macho and Fan 2012ab) to illustrate likely spatial and seasonal patterns in key hydrologic variables.

Figure 1.7. (A) shows the hydrological variability of Amazon; (i) soil water availability to plants mirroring seasonal rain (top), (ii) WTD showing areas of waterlogging (wetland conditions, purple) and root-accessible groundwater (blue) (center), and (iii) flood height showing inun-dation extent and the dynamic nature of lateral connectivity among streams (bottom). These inferred patterns give us glimpses of the large spatial variability and seasonal contrasts in hydrologic conditions across the Amazon. The chemical composition of the waters in the Amazon largely reflects the geologic substrates through which the water flows. The geo chemistry of soil water, particularly soil nutrients for vegetation, which strongly depend on the bedrock (parent material) and geologic age, is dis-

cussed in Section 1.4. Here we highlight the geologic causes for the widely recognized river types across the Amazon (Figure 1.7.B); (a) blackwater rivers originating from lowland forests with sandy soils that are nutrient poor and highly acidic (pH = 3.5–6.0), (b) whitewater rivers sourced in the geologically-young Andean cordilleras, which are sediment- and nutrient-rich and have near neutral pH

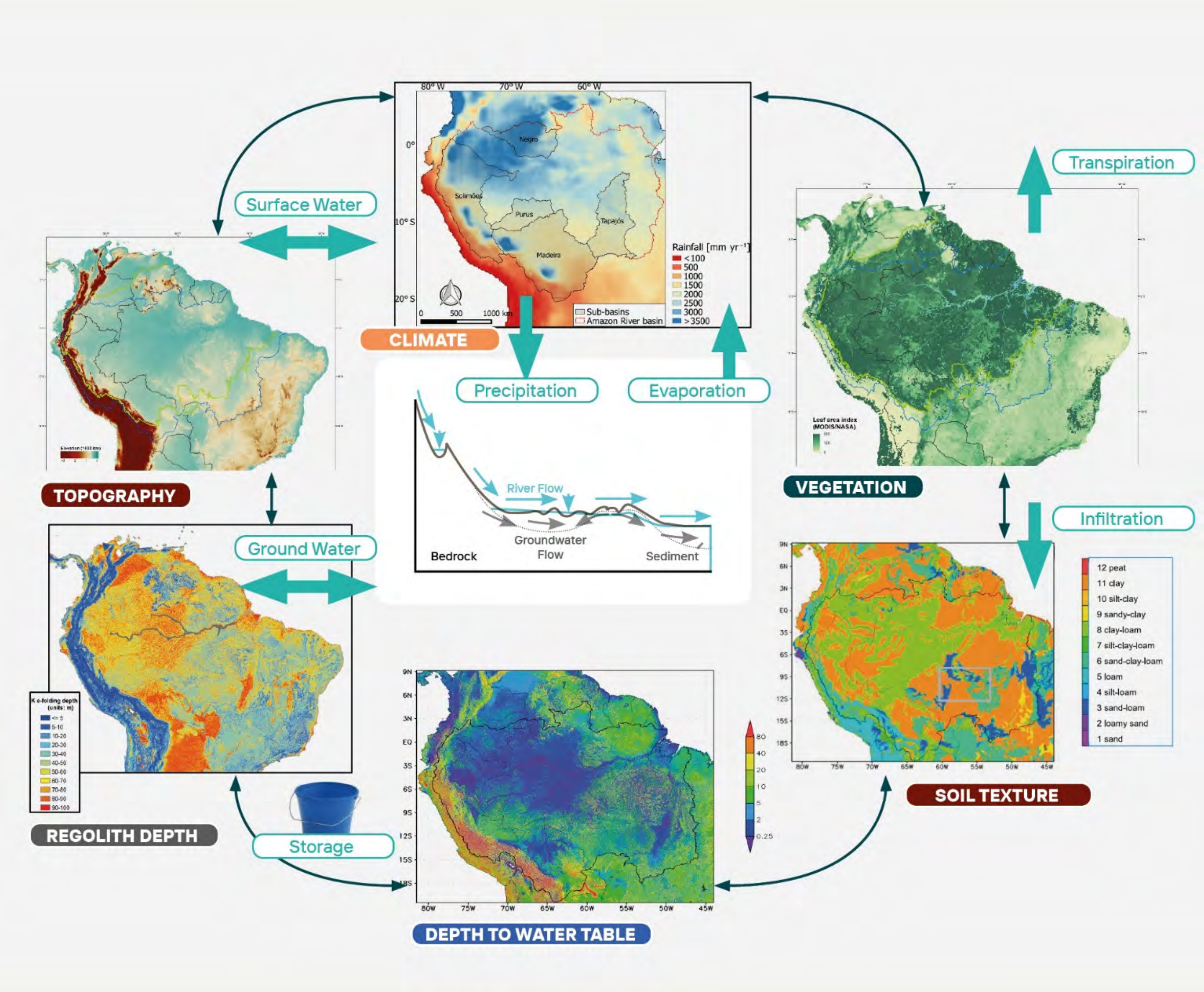


Figure 1.6 Drivers of modern-day Amazonian hydrology. Blue arrows indicate hydrologic effects. Climate (top) determines the precipitation supply and evaporative demand (vertical fluxes). Plant transpiration returns a large portion of the precipitation back into the atmosphere through transpiration (vertical flux), effectively reducing the amount of water to be moved on land laterally. The lateral fluxes are largely controlled by topography via the river network on the surface, and by the terrain-dependent regolith thickness and permeability via groundwater flow in the subsurface. The regolith also controls the storage capacity (the bucket) whereby wet-season surplus is stored and carried over to subsidize dry-season deficits. The soil physical properties control infiltration and hence subsurface storage. All factors influence the water balance of a location directly, but also indirectly via modulating other factors (indicated by double thin black arrows). Sources: climate map from Maeda et al. (2017); vegetation index map from NASA (earthobservatory.nasa.gov/global-maps); topography map from SRTM/NASA (www2.jpl.nasa.gov/srtm); regolith depth map from Fan *et al.* (2013); soil texture map from Miguez-Macho and Fan (2012b); depth to water table map from (Miguez-Macho and Fan 2012b).

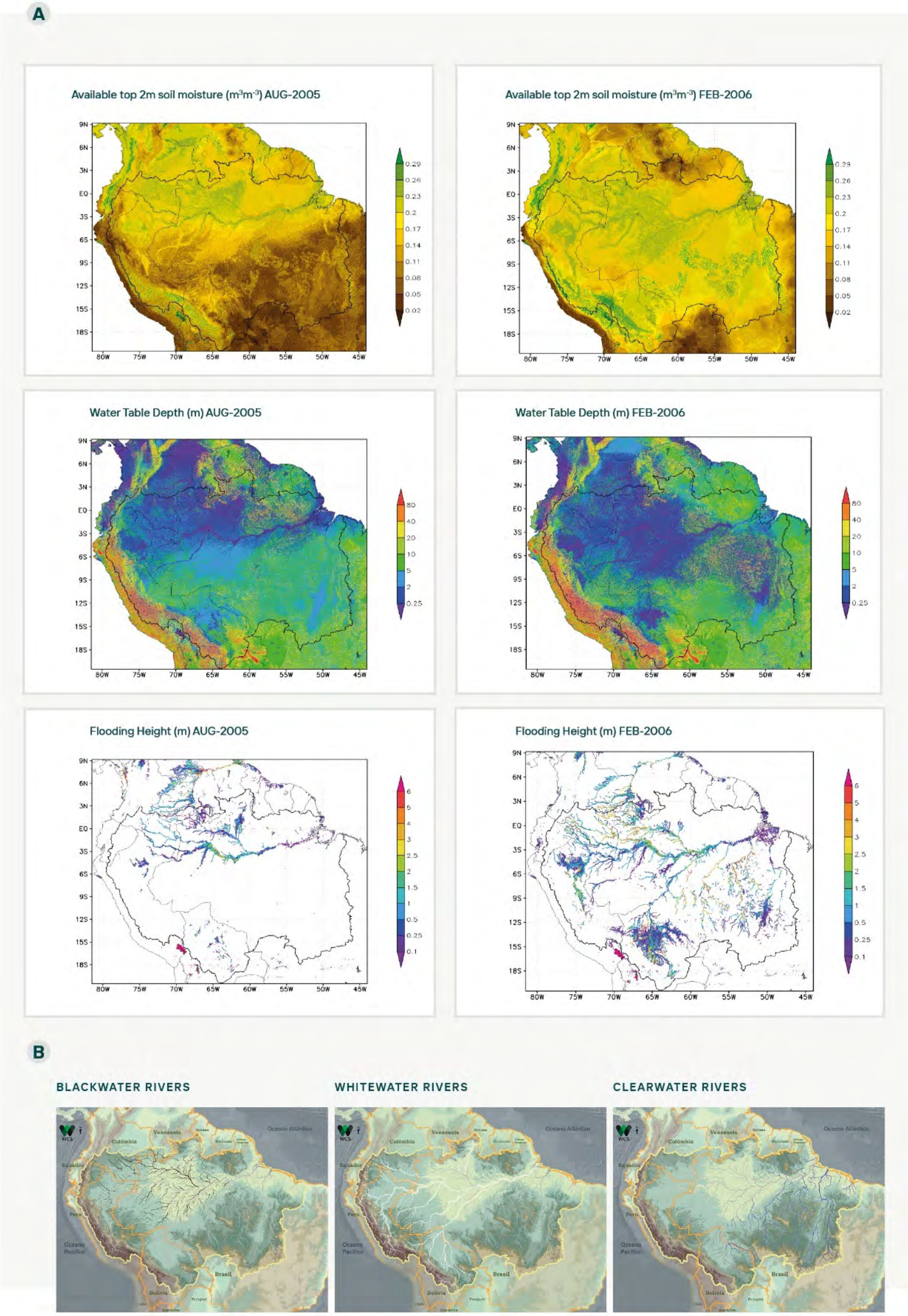


Figure 1.7 (A) Model simulated spatial distribution and seasonal contrast in top 2 m soil moisture (m^{3}m^{-1}) available to vegetation (top); water table depth (middle), flood water height and floodplain connectivity (bottom) (Miguez-Macho and Fan 2012a) (B) Amazon River water types: blackwater, whitewater, clearwater, based on water chemistry and sediment load, reflecting the geochemical nature of their source regions (https://amazonwater.org/waters/rivers-types).

(6.8–7.0), and (c) clearwater rivers that drain the old cratonic shields, which are sediment- and nutrient poor and slightly acidic (pH = 6.1–6.7). Each of these major water types hosts diverse and specialized aquatic plant and animal species (Stefanelli-Silva *et al.* 2019; Albert *et al.* 2020).

Some of the main hydrologic landscapes of the Amazon are periodically flooded wetlands such as *igapó* (blackwater and clearwater) and *várzea* (whitewater), which contrast with the *terra firme* that is never flooded (Figure 1.7.B). It is likely that this diversity has changed in the geologic past as the Amazon's drainage system evolved through millions of years (Section 1.2 and 1.3).

1.5.2 Hydrologic diversity shapes terrestrial and aquatic habitats and ecosystem diversity

The hydrologic variables that matter the most to life include water availability, water quality, temporal stability, and spatial connectivity. The high spatial diversity in water availability and stability is expressed in Figure 1.7.A.

The soil moisture available to vegetation (top row) varies from saturation to wilting point in one season. The water table depth (middle row) varies from 0 to >80 m with contrasting patterns across the season, hinting at seasonal distribution of wetlands, groundwater capillary reaching plant rooting depth, and the thickness and water storage capacity of the vadose zone to be filled in the wet season. The floodwater height (bottom row) is the most dynamic feature of the Amazon, filling and emptying massive floodplains, and seasonally connecting the many channels, enabling migration of aquatic life but hindering that of terrestrial.

At the landscape scale, under the same climate and over similar geology, hydrologic variations strongly align with hillslope gradients, with better-drained hills and poorly-drained valleys. This systematic variation in drainage is the foundation of the topo-sequence or soil catena notion (see Section 1.4). Along the catena, systematic changes in species distribution have been documented, encapsulated in the hydrologic niche concept (Silvertown *et al.* 1999, 2014).

Figure 1.8 gives four examples. In (a), summarizing decades of research in the white-sand ecosystems in Rio Negro drainage, Terborgh *et al.* (1992) notes that the slight undulations in topography, imperceptible on the ground, can dramatically influence vegetation structures, owing to selective vegetation response to water stress (excessively drained sand hills) and waterlogging (shallow water table in valleys), forming elevation zones from *igapó* to *terra firme* forests along a drainage gradient. In (b), the *várzea* forest, tree species richness is strongly zoned along flooding gradients (few species tolerate prolonged flooding) on the floodplains of the lower Solimões River (Wittmann *et al.* 2011). In (c), Schietti *et al.* (2014) found that species turnover corresponds to turnovers in water table depth, from uniformly deep under the plateaus (10% species turnover), to varying and fluctuating near the valleys (90% species turnover). In (d), along a hillslope in the Brazilian Cerrado, a denser and more complex woody canopy occupies the well-drained upper slopes, and the shallow water table under the lower slopes causes waterlogging and restricts species occurrence (Rossatto *et al.* 2012). The significance of hillslope drainage is greater in the parts of the Amazon with a strong dry season, when valleys remain moist and can sustain floristically different valley ecosystems.

1.6. Mineral Richness, Hydrocarbons, and Aquifers in the Amazon

The Amazon has long been known as an area of high potential for mineral resources and represents one of the last mineral exploration frontiers in the world (Cordani and Juliani 2019). In recent decades, the region has been the locus of intense mining activities (Monteiro 2005; see Chapters 9 and 11), including the districts of Carajás for Fe, Cu, Au, Mn, and Ni; Pitinga for Sn, Nb, and rare earth elements (REE); Serra do Navio for Mn; and Trombetas-Juruti for Al (See table in Figure 1.9). Mineral exploration of the Amazon had long been dominated by *garimpos* (i.e., small-scale, largely unregulated mining operations). Starting in the 1990s, large mining companies began employing modern technologies, such as operations in the Carajás Province (Fe, Cu and Mn) and Juruti-Trombetas (Al) (Monteiro 2005; Cordani and Juliani 2019).

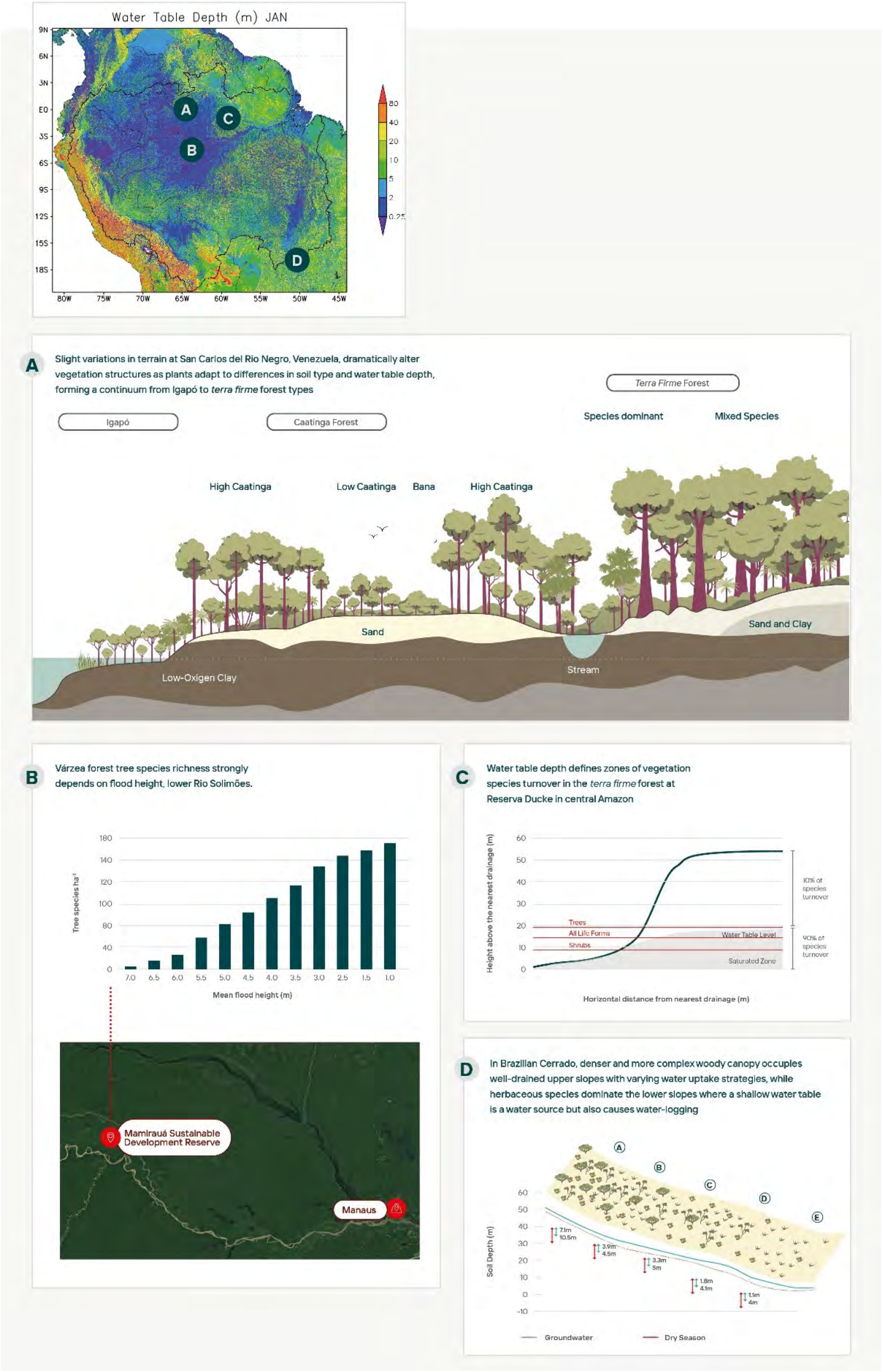


Figure 1.8 Examples of hydrological influence on species distribution at landscape scales in the Amazon. Source: (A) Terborgh *et al.* (1992); (B) Wittmann *et al.* (2010); (C) Schietti *et al.* (2014); (D) Rossatto *et al.* (2012).

New frontiers for mineral exploration encompass the central area of the Amazon Craton on the Brazilian Shield, particularly in the Ventuari-Tapajós and Rio Negro-Juruena provinces (Juliani *et al.* 2016)

The rush for precious and base metals has attracted many international mining companies to the Amazon. Nevertheless, the subsurface geology and mineral potential remains poorly known throughout much of the lowland Amazon and the Guiana Shield. These regions are difficult to access and have long experienced complex political and social issues related to industrial development.

The sedimentary basins of the Amazon contain large formations with significant porosity and permeability. A recent synthesis of multiple data sources in the western Amazon suggests that the Amazon Aquifer System (AAS) is potentially one of the largest aquifer systems in the world (Rosario et al. 2016) as discussed in Section 1.6.3.

1.6.1 Ore Deposits in the Amazon: A Diversity from the Archean to the Phanerozoic

Ore deposits are anomalous concentrations of an element of economic interest within the Earth's crust. Ore deposits may form as a result of (i) interaction of the lithosphere, hydrosphere, atmosphere, and biosphere; (ii) decrease in internal global heat production, and (iii) changes in global tectonics (Robb 2005). The great variety of Amazonian ore deposits is a consequence of the complex and protracted geological evolution described in this chapter.

Amazonian ore formation began as early as the Mesoarchean (c. 3.0 Ga), with geological processes during the Phanerozoic enlarging the mineral potential of the region. Most known Amazonian ore deposits are concentrated in Precambrian terranes, whereas hydrocarbon and aquifer resources are concentrated in Phanerozoic sedimentary basins (Figure 1.9, Figure 1.2A and B). One of the most prolific mineral provinces in the world is located within the oldest core of the Amazonian Craton, in the Archean Carajás Province. In the southern part, in the Rio Maria Domain, the metallogenesis of the terrain is marked by the occurrences of some gold deposits within Mesoarchean (3.2–2.8 Ga) greenstone belts (Monteiro *et al.* 2014). Conversely, in the northern part of the Carajás Province, the Carajás Domain is one of the best-endowed mineral provinces in the world with a wide variety of ore deposits (Monteiro *et al.* 2014). Iron deposits associated with banded iron formations in Carajás are globally recognized as the largest mining operations in the world. Manganese deposits, such as at the Azul Mine, also occur in Carajás. Additionally, in recent years, Carajás also became a relevant copper (with associated gold) producer in Brazil (Juliani *et al.* 2016). Widespread mafic or ultramafic rocks host remarkable Ni and PGE (Platinum Group Elements, e.g., Pt and Pd) deposits also in the Carajás Mineral Province. During the Transamazonian Orogeny (c. 2.05 Ga) substantial Mn deposit formed in the Maroni-Itacaiúnas Province, such as the Buritirama and the Serra do Navio.

It is common to find a wide variety of granite-related ore deposits associated with paleo-subduction zones within the Paleoproterozoic terranes (2.1–1.6 Ga). The Tapajós Mineral Province and the Alta Floresta Gold Province are the current frontiers of mineral exploration in Brazil (Juliani *et al.* 2016; Klein *et al.* 2018). In these settings, plutono-volcanic rocks hosting different styles of Au-Ag-Cu-Mo deposits of Paleoproterozoic age are encountered. Towards the northwestern portion of the Alta Floresta Gold Province, the Aripuanã mine is a rare example of a Paleoproterozoic Pb-Zn deposit associated with preserved volcanic calderas (Biondi *et al.* 2013).

In the northern sector of the Ventuari-Tapajós Province, in the Guiana Shield, granite-related ore deposits are also reported, including (i) the famous Pitinga deposit, a historical mine of Sn with large contents of Nb, Ta, F, and REE (Bettencourt *et al.* 2016); and (ii) the Surucucu district, a poorly investigated terrain with Sn and Au deposits (Klein *et al.* 2018). At the interface of the Rio Negro-Juruena and Rondoniana-San Inácio provinces, in the southwestern portion of the Amazon Craton, remarkable Sn deposits were discovered and exploited in the last 50 years (Bettencourt *et al.* 2016). The intrusion of granites from 1.31–0.97 Ga gave origin to great deposits of Sn, W, and Nb (Bettencourt *et al.* 2016). The Seis Lagos deposit represents one of the most important Nb and REE reserves in the world. This ore deposit is contained in a carbonatite intrusion and forms part of the northern Rio Negro-Juruena Province, with an age of about 1.3 Ga (Rossoni *et al.* 2017).

Aluminum deposits (bauxite ores) are quite common in the Amazon and encompass large reserves. The Trombetas-Juruti and Parago-minas bauxite districts represent important sources of aluminum and are found in low relief plateaus within some of the Phanerozoic sedimentary basins (Costa 2016; Klein *et al.* 2018). These deposits are also a good example of ore deposits formed by extreme weathering and leaching of undesired elements, which concentrate metals in the sedimentary matrix. Mature lateritic cover is a common feature in the Amazon, which was formed by intense weathering processes due to climate conditions. These processes are thought to have begun at c. 80 Ma and remain active to the present (Monteiro *et al.* 2018). Importantly, these processes also enhance the quality of the Fe deposits of Carajás, the Mn deposits at Buritirama and Serra do Navio, and the Nb-REE deposits at Seis Lagos.

1.6.2 Oil and gas

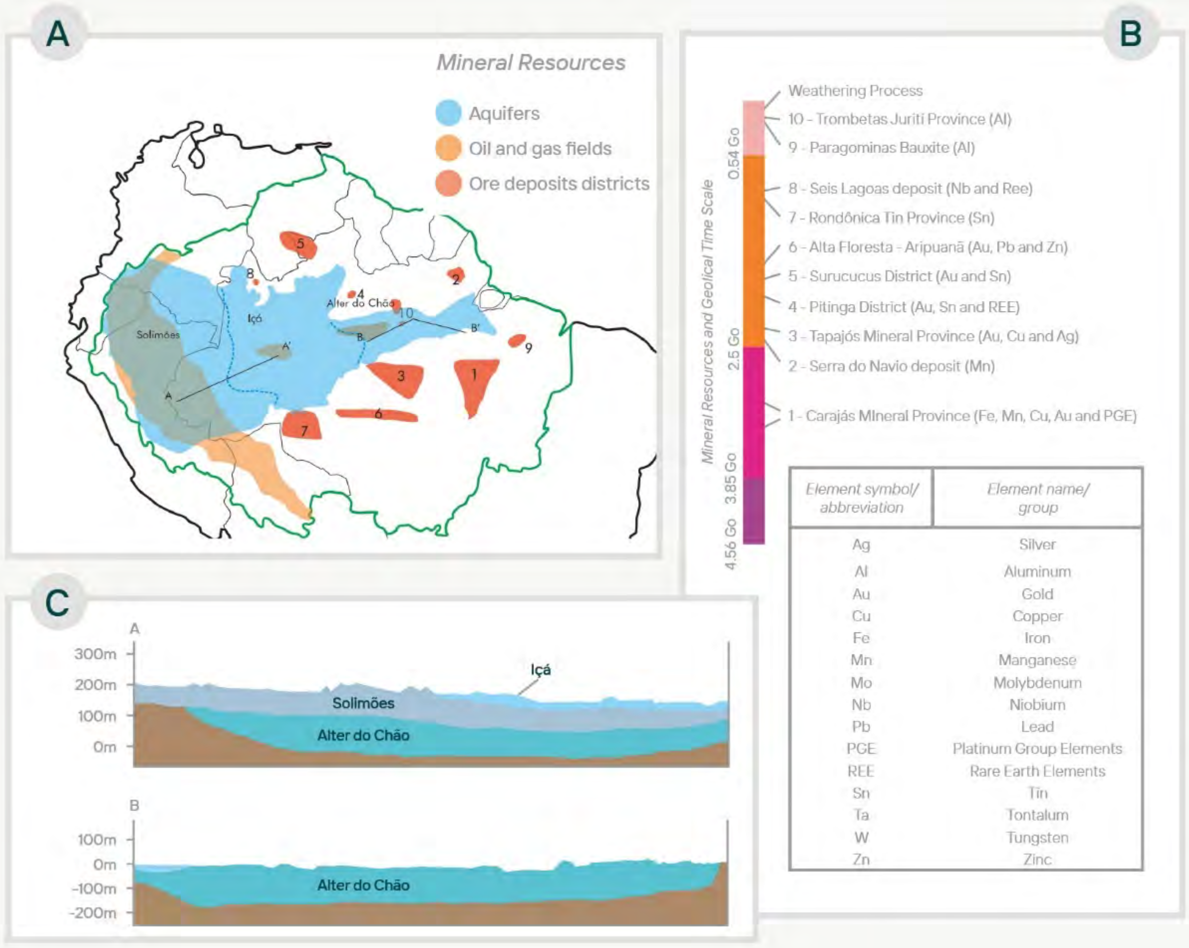
Oil and gas are mainly concentrated in the Subandean region, along the western margins of the Amazon, and to a lesser extent in the western and eastern Amazon (Figure 1.9). In Subandean sedimentary basins, the search for oil and gas started during the 1940s; however, the first oil reserves were not discovered until the 1980s in the Llanos region of Venezuela. Subsequently, hydrocarbon exploration expanded south from Colombia into Ecuador and Peru. The greatest proven hydrocarbon reserves are now known to occur in the westernmost Amazon, at the foothills of the Andes (de Souza 1997).

In the Brazilian Amazon, the search for oil and gas started during the 1950s in the intracratonic sedimentary basins, a very different type of geological and geographical setting. Initially, exploratory activity was focused on the banks of major rivers, such as the Solimões-Amazon, Tapajós, and Madeira. Later, exploration expanded into the forest. In 1978 the Juruá gas field was discovered by Petrobras (the state-owned Brazilian oil company). In the following years three appraisal wells were drilled in the Juruá field aiming to assess its potential, which was determined non-commercial. Nevertheless, at the beginning of the 1980s, Petrobras started a new exploratory campaign which eventually led to the discovery of the oil and gas field of Rio Urucu in 1986, deep in the hinterland of the western Amazon and in the Solimões sedimentary basin. As this new field contained oil in addition to gas, Petrobras redirected its exploratory efforts to this new area, leaving the development of the Juruá gas field for future demands, but conditioned to the potential of new discoveries and the commercial demand for dry gas. Following the Rio Urucu discovery, an even bigger oil and gas field named Leste de Urucu field was discovered. Other smaller oil and gas fields surrounding the Urucu oil and gas Province were discovered during the 1990s (Souza, 1997). Today, a private company holds a monopoly over exploration and exploitation of the oil and gas in the Brazilian Amazon.

1.6.3 Aquifers

Major aquifer systems in the Brazilian Amazon are shown in Figure 1.9. The largest are found in sedimentary basins along the main stem of the Amazon River, comprising the Amazonas sedimentary basin to the east and the Solimões sedimentary basin to the west. Here, thick sequences of sand and clay deposits formed during the Mesozoic and Cenozoic allow for the accumulation of large, continuous aquifer systems (alternating aquifers and confining units) (Figure 1.9). In map view (A), they are from east to west the Alter do Chão, Içá, and Solimões aquifer systems (Rosário *et al.* 2016; Hu *et al.* 2017). The cross-section view (B) illustrates the aquifer types, where the surficial exposed (unconfined) aquifers are actively recharged by precipitation and discharge into the river drainage network, but the buried (confined, if buried under low-permeability strata) aquifers are isolated from the surface waters. Off the central axis of sedimentary basins, along the main stem of the Amazon River, are the small aquifers of Boa Vista and Parecis (not shown) in fractured Paleozoic sandstones/siltstones (Hirata and Suhogusoff 2019), which have limited groundwater storage capacity.

While the Alter do Chão aquifer is largely unconfined in the eastern Brazilian Amazon (section B-B’, Figure 1.9.B), it becomes semi-confined in western Brazil under the Içá and Solimões aquifers (section A-A’). The Solimões aquifers in the western Amazon are unconfined, exchanging water with the river network (Rosário *et al.* 2016). Through a synthesis of multiple data sources, Rosário *et al.* (2016) also identified the confined Tikuna aquifer system, a large, continuous, Cretaceous sandstone unit in the Solimões Basin (see their Figure 10). The Alter do Chão Formation is ex-



Element symbol/ abbreviation	Element name/ group
Ag	Silver
Al	Aluminum
Au	Gold
Cu	Copper
Fe	Iron
Mn	Manganese
Mo	Molybdenum
Nb	Niobium
Pb	Lead
PGE	Platinum Group Elements
REE	Rare Earth Elements
Sn	Tin
Ta	Tontalum
W	Tungsten
Zn	Zinc

Figure 1.9 (A) Simplified tectonic-chronological map of northern South America with the distribution of the main ore deposits and oil and gas fields (Modified from Marini *et al*. 2016, and Klein *et al*. 2018). (B) Ore deposits of the Amazon and their location across the geological time scale. Also shown in (A) are major aquifer systems with cross sections shown in (C) (modified from Rosário *et al*. 2016; Hu *et al*. 2017).

posed in the eastern Amazon and continues westward from the Amazonas to Solimões sedimentary basins, where it has been assigned two aquifer names: Alter do Chão (Amazonas sedimentary basin) to the east where it is exposed, and Tikuna (Solimões sedimentary basin) to the west, where it is buried. Three aquifers are stacked vertically: the Içа, Solimões, and Tikuna (or Alter do Chão). Together, these large sedimentary aquifers make up the Amazon Aquifer System, one the largest aquifer systems in the world (Rosário *et al.* 2016).

1.7 Outlook: The Future of the Amazon

Amazonian geodiversity faces grave and imminent threats from a broad range of human activities. These threats range from deforestation due to dam and road construction, mineral extraction, and associated land-use changes, to global climate change and sea level rise. Under "business as usual" models of carbon emissions, global temperatures are predicted to rise 6°C by 2100 (IPCC 2021), but regional changes in temperature and related ecosystem responses can differ spatially, especially in topographically-rich areas such as the Andes (IPCC 2021). Anthropogenic global warming is already having dramatic environmental consequences for Amazon, with the greatest future impacts resulting from sea level rise and pronounced shifts in rainfall patterns and intensities. Currently, the Earth's atmosphere averages 416 ppm CO_2, a concentration 150% above the maximum amount measured during the Pleistocene (Glacial - Interglacial) cycles of the past 2.6 million years, and representing a level not seen since the early Miocene c. 23 million years ago (Cui *et al.* 2020).

Paleoclimatic data and climate modelling indicate that high global mean surface temperatures previously occurred in earlier geological epochs (e.g., Inglis *et al.* 2020). For example, the Paleocene-Eocene Thermal Maximum (PETM, about 56 Ma) is an excellent analogue for our post-industrial fast-warming world (McInerney and Wing, 2011; Jones *et al.* 2019). Similarly, the Early Eocene Climatic Optimum (EECO c. 53–51 Ma) also represents a useful historical analogue for future scenarios, due to similarly high concentrations of atmospheric CO_2 (Inglis *et al.* 2020). Recent climate models by Inglis *et al.* (2020) suggest that during the PETM and EECO the Earth's global mean surface temperatures were respectively 31.6°C and 27°C. When assuming a pre-industrial temperature of c. 14°C, this makes the PETM and the EECO respectively c. 17.6°C and 13°C warmer than pre-industrial levels.

If carbon emissions continue unabated, Amazonian climates will be dramatically altered by 2100 (Sorribas *et al.* 2016). Melting polar ice caps will contribute to more than 13 m (c. 43 ft) global sea level rise by 2500 (DeConto and Pollard 2016), and complete loss of the Earth's ice caps is projected within the next 400–700 years (Winkelmann *et al.* 2015; Foster *et al.* 2017). In an ice-free world, global sea levels will be c. 60–80 m (c. 200–260 ft) above the present level (Winkelmann *et al.* 2015), higher than they have been for c. 56 million years (Foster *et al.* 2017; Tierney *et al.* 2020). These projections imply that marine waters would be driven deep into the Central Amazon, dramatically altering shorelines, habitats, microclimates, and regional rainfall patterns (Figure 1.10). Such a marine incursion would convert more than one million km^2 of lowland Amazonian rainforest estuarine and marine habitats, inundating the full geographic range of at least 1,030 plant species that are entirely confined the lowlands and the eastern Amazon, and possibly driving most if not all these species to extinction (Zizka *et al.* 2018).

During the Middle Miocene Climate Optimum (MMCO; c. 17–15 Ma) global mean surface temperatures were estimated to have been 18.6°C, which is c. 3°C higher than present (You *et al.* 2009). This makes the MMCO a realistic analogue for global temperatures and sea levels in the next century. During the MMCO, much of the western Amazon was covered by the Pebas mega-wetland system, with estuarine conditions caused by marine incursions related to the prevailing high sea level (Hoorn *et al.* 2010b; Jaramillo *et al.* 2017 Fig. 1.4.C.). Although basin dynamics in the western Amazon were different during the MMCO, overall, the geo-

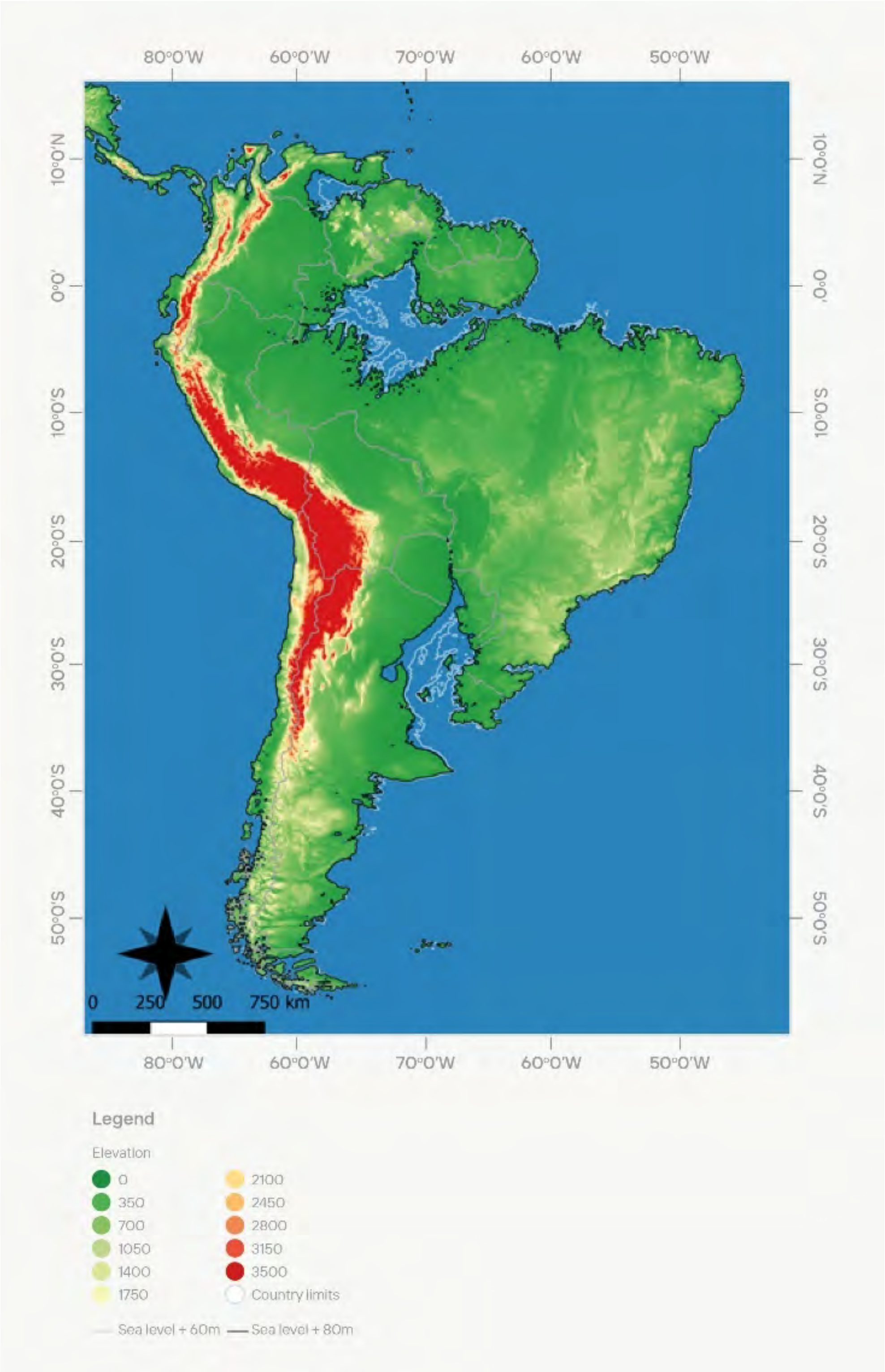


Figure 1.10 Projected coastline of South America after Earth's ice caps have melted (c. 2400 to 2700 CE) with shorelines antecipated at 60 and 80 m (216 and 262 ft) elevation. Image courtesy of Dr. João Marcelo Abreu, Universidade Federal do Maranhão, Brazil.

logical past can provide modern scientists insight into how future landscapes may unfold under climate scenarios of global warming.

The scientific community is currently unable to accurately predict in detail how Amazonian landscapes and riverscapes will respond to all these simultaneous challenges. We simply do not have the data to forecast all the effects of encroaching shorelines, increased extreme flooding and rainfall, severe droughts, and reduced vegetation. Nonetheless, we can expect intensified erosion of bare soils, increased debris in rivers, and erosion of river margins. Rivers will become even more prone to flash floods. Fires will increase these effects in a positive feedback loop, leading to higher fire probability due to diminished vegetation cover promoted by soil erosion and regional aridification, particularly in the headwaters of the main southeastern tributaries (e.g., Tapajós, Xingu, Tocantins) (Flores *et al.* 2019; Brando *et al.* 2020a, b). Regime shifts in landscape vegetation cover are already being observed in other parts of the world following a series of devastating fire seasons, such as those in Australia (Filkov *et al.* 2020), California (Wahl *et al.* 2019) and the Mediterranean (Camarero *et al.* 2019), among many others.

Facing so many environmental crises at once, the Amazon is precipitously on the edge of an evolutionarily unique climatic regime shift, an irreversible change from mostly forested to mostly open and environmentally degraded agricultural, marginal, and abandoned landscapes (Munroe *et al.* 2013; Xu *et al.* 2020). Future Amazonian landscapes may look very different from the vast tropical rainforests that have covered most of the region for the past 100 million years. Anthropogenic deforestation and habitat degradation in other parts of the world have already transformed large blocks of ancient forests into agricultural and marginal landscapes over the past few decades and centuries. These deforestations resulted in widespread soil erosion, aridification, and biodiversity loss, for example in the Mississippi and Yangtze river valleys. Immediate and sustained investments are required to support climate mitigation and landscape conservation policies, with coordinated actions at the local, national, and international levels (Albert *et al.* 2020).

To summarize, there is broad consensus within the geoscience and climate science communities that maintaining the Earth's polar ice caps is critical for the persistence of the relatively stable climates and shorelines that support modern ecosystems and human civilization (Sigmond *et al.* 2018; Vousdoukas *et al.* 2018; Westerhold *et al.* 2020, Lear *et al.* 2021). In the starkest of terms, we risk raising the concentration of CO_2 in the Earth's atmosphere above 450 ppm at our peril (Sherwood *et al.* 2020). Studies into the dynamics of Amazonian geodiversity are still in their infancy, and quantitative attention to Amazonian earth systems dynamics will be required to effectively manage Amazonian landscapes through the perilous decades and centuries to come. The projected dire impacts of climate change described here may be underestimated, as we do not have a robust understanding of the interlinks and cascading effects that rising global temperatures will have on the environment.

1.8 Conclusions

In this chapter, we explored the origins of the Amazon's geodiversity, with the aim to unravel links between geological history, climate, geomorphology, soils, hydrology, and biodiversity. We found deep connections between these seemingly independent components in the region.

The most striking point that we convey through this multidisciplinary study is that Amazonian history unfolded over the course of 3 billion years. During this time, the geological substrate of the Amazon region formed part of different continents, with the current configuration only taking shape in the past 100 million years. Key geographic features such as the Andes mountains at the western margin of the Amazon, and the connection between South and Central America were only completed in the past 20 million years. Conversely, the building blocks of the eastern Amazon were configured between 3 and 1 billion years ago. The timing of these configurations (west and east) and their legacy effects, such as the stability of the eastern Amazon and mountain building in the western Amazon, were largely dictated by the movement of tectonic plates. The interconnection between these 'old' and 'young' crustal regions is what makes the Amazon unique. For example, the east-west gradient of geological province ages is reflected in soil types, which in turn creates gradients in soil nutrients and, therefore, ecosystems. The overall distribution of rain in the Amazon is directly shaped by the Andes which, along with soil types, interconnect to affect hydrological conditions in the lowlands. Climate, soils, hydrology, mineral and hydrocarbon wealth, and biodiversity are either derived from or superimposed on this diverse geological tapestry crafted by geological time.

The Amazon's rich geological history can be partly gleaned from deep records in its intracontinental sedimentary basins and offshore deposits. These records provide a consistent, albeit incomplete, picture of what the environment looked like from millions to tens of millions of years ago, when sea levels and global climate were drastically different. These records demonstrate that, while part of the rich geological tapestry was set over billions of years, the environmental, climatic, and landscape changes in this region were dynamic and pervasive over tens of millions of years. While these data help us understand environmental and climatic changes over the million-year timescale in the Amazon, the feedbacks between geological and climatic processes which dynamically shape the environment require temporal resolutions of at least tens of thousands of years. Sedimentologic and paleoclimatic records with high temporal resolution are scarce and restricted to caves, lakes, and glacial cores high in the Andes. Their unfortunate scarcity is matched with abundant need for more data. High-resolution records are crucial to comprehending the Amazon's response to extreme climatic fluctuations.

Only by understanding intricate connections like the ones summarized here can we provide a basis for future management and conservation plans. However, as demonstrated in this Chapter, this is no trivial task. Historical archives of a dynamic past also constitute our guidelines for the future and are, therefore, paramount for drawing management strategies. Past changes in climate and sea level help us envision the future, if scenarios drawn by the IPCC become reality. Nevertheless, for many factors, such as rates of soil and forest degradation, there are no analogues and we could experience changes to the landscape that are not easily repaired.

The best strategies to reduce human impacts on the natural environment are undoubtedly based on scientific information. Our recommendations are, therefore, to cast a wide scientific net to produce a deeper understanding of the Amazon system.

1.9 Recommendations

The global community must work closely and swiftly with Amazonian governments to develop and enact the following scientific priorities.

- Decade-level financial investments and political support for geoscientific research in the Amazon, prioritizing research and education at institutions that enable the study of Amazonian geodiversity at multiple spatial and temporal scales and across social boundaries; this includes training the next generation of Amazonian geoscientists.
- Interdisciplinary studies of Amazonian earth systems, focusing on interactions among landscape, climate, and biological processes, and how complex feedback loops among these systems are affected by ongoing anthropogenic influences.
- Integrating "big data" from all of the environmental sciences (e.g., geoscience, climate, biology), with emerging tools and expert knowledge to develop new technologies for

environmental characterization, including especially soil and aquatic (surface and subsurface) geochemistry.

- Establish a network of Critical Zone Observatories (*sensu* Brantley *et al.* 2017) in the Amazon to advance study of landscape evolution processes, erosion rates, and sediment yield, over historical and geological timescales, crucial to predicting future geomorphic responses to accelerating environmental change and human-built infrastructure.

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Amazon Assessment Report 2021

Chapter 2

Evolution of Amazonian biodiversity

Dentro da Reserva de desenvolvimento Sustentável (RDS) Vitória de Souzel 2017 (Foto: Lilo Clareto/Amazônia Real)

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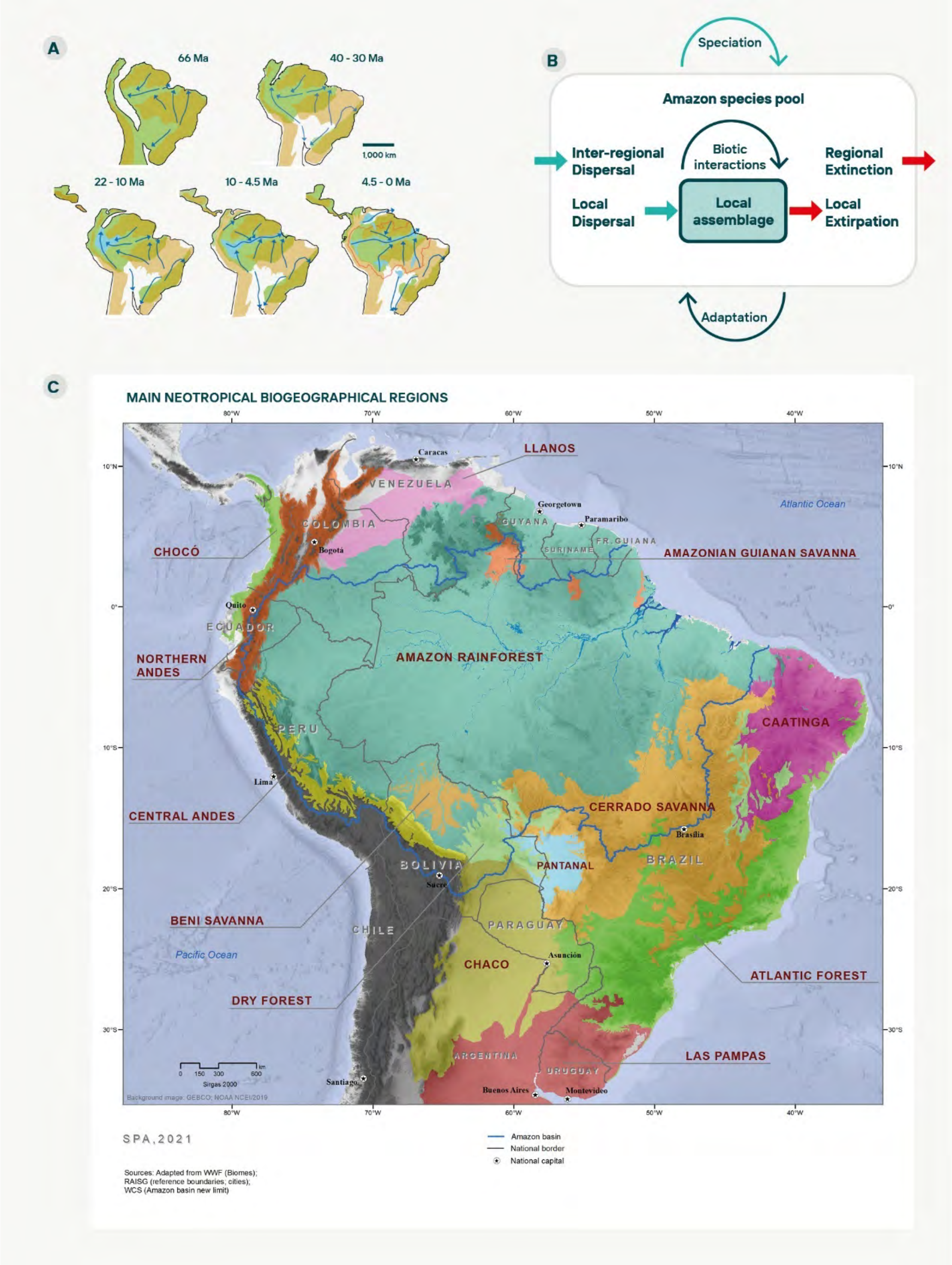
Graphical Abstract



MAIN NEOTROPICAL BIOGEOGRAPHICAL REGIONS

Sources: Adapted from WWF (Biomes); RAISG (reference boundaries; cities); WCS (Amazon basin new limit)

Figure 2.A Graphical Abstract

Evolution of Amazonian Biodiversity

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Key Messages

- Amazonian biodiversity is vast, with the highest species density on Earth, yet remains poorly known at many levels.
- Amazonian biodiversity is heterogeneously distributed, with many distinct ecosystems and environments that harbor unique ecological and evolutionary processes. Many biodiversity patterns (e.g., richness, endemicity) are unique to certain taxonomic groups and cannot be generalized.
- Amazonian biodiversity accumulated incrementally over tens of millions of years, by the action of natural processes operating across the vast spatial scale of the entire South American continent. In this sense, Amazonian biodiversity is irreplaceable.
- The origin of new species is influenced by historic and current variation in geography, climate, and biotic interactions. Speciation time widely varies among taxonomic groups.
- Unlike other regions of the Earth, Amazonian species and ecosystems escaped the regional scale deforestation and defaunation of the Pleistocene ice ages. Amazonian biotas are relatively intact as compared with their high latitude counterparts in North America and Eurasia, or in the more naturally aridified regions of tropical Africa and South Asia. Tropical South America is unique in having retained into the modern era the most diverse set of terrestrial ecosystems on Earth.
- Amazonian species interactions are extraordinarily complex, and increasingly imperiled in the face of immense and accelerating anthropogenic environmental impacts.
- Amazonian biodiversity resulted from a long and dynamic history of environmental change and biological interactions operating over millions of years. Maintaining the evolutionary and ecological processes that result in biological diversification and adaptation is fundamental for the survival of this ecosystem and its critical ecological and economic functions, both regionally and globally.

Abstract

The Amazon constitutes the greatest concentration of biodiversity on Earth, with >10% of the world's described species compressed into only about 0.5% the Earth's total surface area. This immense diversity of

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life forms provides unique genetic resources, adaptations, and ecological functions that contribute to ecosystem services globally. The Amazon's biota was assembled over millions of years, through a dynamic combination of geological, climatic, and evolutionary processes. Its singular history produced heterogeneous landscapes and riverscapes at multiple geographic scales, generated diverse habitats, altered the geographic and genetic connections among populations, and impacted rates of adaptation, speciation, and extinction. Its ecologically diverse biota in turn promoted further diversification, species coexistence, and coevolution, increasing biodiversity over time. Important events in Amazonian history included (i) the late Cretaceous and early Paleogene origins of major rainforest plant and animal groups (ca. 100-30 Ma); (ii) a global cooling event at ca. 30 Ma, in which rainforests contracted to tropical latitudes, during which the Amazon and Atlantic rainforests were first separated; (iii) the uplift of the Northern Andes (especially in the last ca. 20 Ma), which separated the Chocóan and Amazonian lowland rainforests and created new environmental conditions for colonization and speciation, formed mega-wetland systems in the western Amazon, and contributed to the origin of the modern transcontinental Amazon River; (iv) the closure of the Central American Seaway and the formation of the Panamanian Isthmus during the Miocene and Pliocene Epochs (ca. 15-3.5 Ma), which facilitated the Great American Biotic Interchange; and (v) the climate oscillations of the Pleistocene ice ages (2.6-0.01 Ma), followed by human colonization and associated megafaunal extinctions. Human activities have impacted Amazonian ecosystems for >20,000 years, accelerating over the past 400 years and especially the past 40 years, now posing existential threats to Amazonian ecosystems. Amazonian conservation requires documenting its diverse biota, and monitoring the biogeographic distributions of its species, species abundances, phylogenetic diversity, species traits, species interactions, and ecosystem functions. Decade-scale investments into biodiversity documentation and monitoring are required to leverage existing scientific capacity. This information is key to developing strategic habitat conservation plans that will allow continuity of the evolutionary and ecological processes taking place across the Amazon basin, now and into the future.

Keywords: adaptation, biodiversity, biogeography, coevolution, conservation, ecology, extinction, Neotropics, speciation, South America.

2.1 The Amazon River Basin

Chapter 1 provides a synthetic overview of the geological processes and time scales in which the Amazonian region was formed, illustrating how Amazonian landscapes were assembled by geological and climatic processes operating over millions of years. The modern trans-continental Amazon River Basin was formed during the past 10 million years, draining an area bounded by the Andes to the west, and the Guiana and Brazilian shields to the north and south, respectively. This drainage basin is the largest on Earth, including the Tocantins-Araguaia and adjacent coastal basins of northern Brazil. It covers a total area of about seven million km^2 or about 40% of South America, and discharges about 16–20% of the Earth's total freshwater to the sea, depending on the year (Richey *et al.* 1989). Most of the Amazon basin is covered by humid lowland tropical rainforests, representing the largest contiguous area of tropical rainforest in the world. The Amazon rainforest ecosystem, including adjacent areas of the Guiana Shield, also covers a total of about seven million km^2 (Figure 2.1).

2.2 Amazonian Biodiversity is Immense and Vastly Underestimated

Organismal diversity of the Amazon Basin is among the highest on Earth (Bass *et al.* 2010). Approximately 10% of the world's vertebrate and plant species are compressed into an area that corresponds to ca. 0.5% of the Earth's total surface (Jetz *et al.* 2012; Tedesco *et al.* 2017; Ter Steege *et al.* 2020, Figure 2.2). Amazonian diversity also represents a bewildering range of life forms, ecological functions, chemical compounds, and genetic re-

Figure 2.1 The Amazon River drainage basin (thin blue polygon) and the original distribution of the main Neotropical biogeographic regions. Note that the Seasonally Dry Diagonal region (composed of the Caatinga, Cerrado, and Gran Chaco) separates the Amazon and the Atlantic rainforests, while the Northern Andes separates the Amazon and the Chocó rainforests.

sources (Darst *et al.* 2006; Asner *et al.* 2014; Albert *et al.* 2020a, Figure 2.3). These highly diverse Amazonian ecosystems constitute the core of the Neotropical realm, which harbors ca. 30% of all species of vascular plants (Raven *et al.* 2020), vertebrates (Jenkins *et al.* 2013; Reis *et al.* 2016), and arthropods (Stork 2018) on Earth (detailed data about the richness of Amazonian species is provided in Chapter 3).

Despite decades of intensive study, the full dimensions of Amazonian diversity still remain vastly underestimated (da Silva *et al.* 2005; Barrowclough *et al.* 2016; García-Robledo *et al.* 2020). This underestimation results from the extremely high number of species found in the region (Magurran and McGill 2011; Raven *et al.* 2020), the numerous species yet unrecognized due to their subtle phenotypic differences (Angulo and Icochea 2010; Benzaquem *et al.* 2015; Draper *et al.* 2020), the logistical difficulties with sampling in remote regions (Cardoso *et al.* 2017; Ter Steege *et al.* 2020), collection efforts that are biased towards accessible localities (Nelson *et al.* 1990; Hopkins 2007; Loiselle *et al.* 2008), and a disproportionate number of studies of conspicuous organisms (Ritter *et al.* 2020) and broadly distributed species (Ruokolainen *et al.* 2002). As a result, many Amazonian species have never been collected, named, or studied; often, an entire group of closely related species (i.e., clade) is

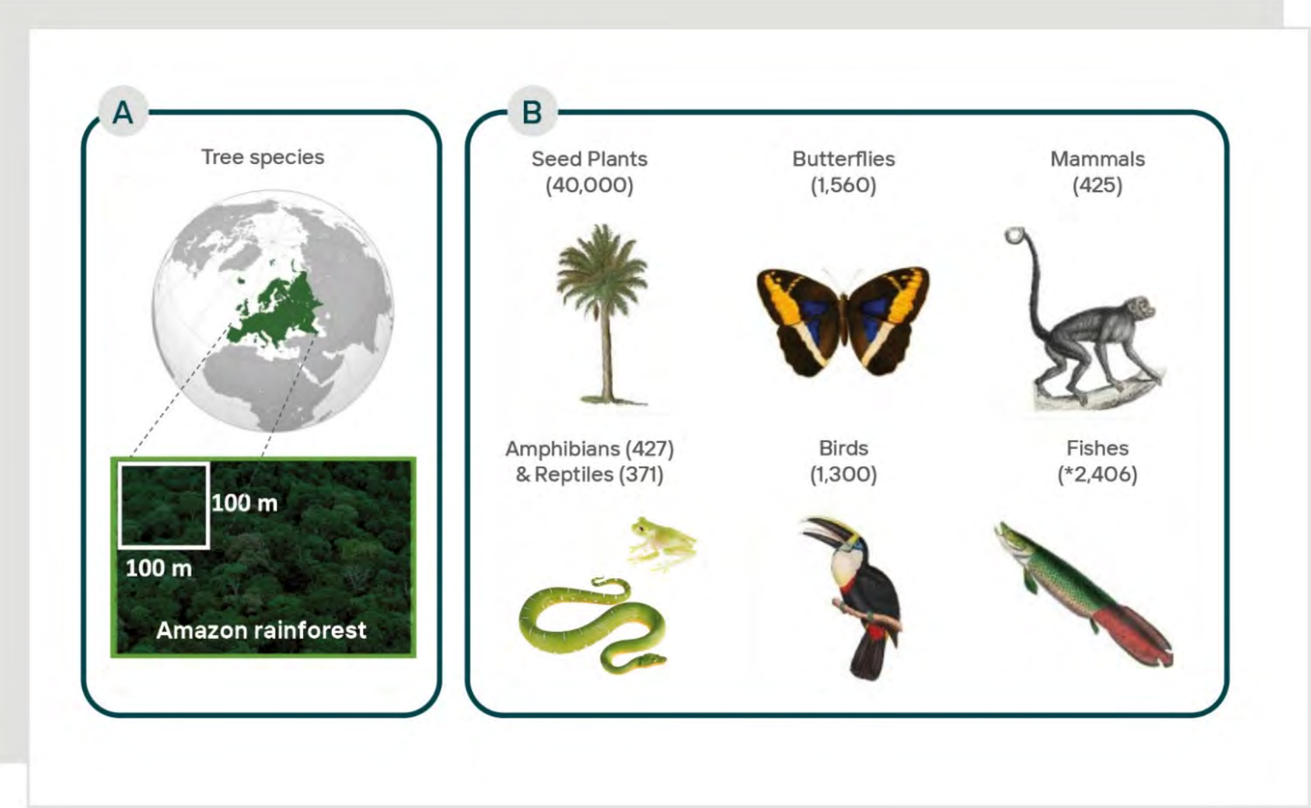


Figure 2.2. The Amazonian lowlands in numbers (minimum estimates based on current knowledge). A. More trees species are found in a 10,000 m^2 area of Amazon rainforest than in the whole of Europe (Ter Steege *et al.* 2006). B. Estimated numbers of species of selected Amazonian lineages, including vascular plants (Hubbell *et al.* 2008; Mittermeier et al. 2003; image by Roberts 1839), butterflies (Vieira and Höfer 2021; image by Hewitson 1856), mammals (Mittermeier *et al*. 2003; image by Jardine *et al.* 1840), amphibians and reptiles (Mittermeier *et al.* 2003; image by Jose Vieira / Tropical Herping), birds (Mittermeier *et al.* 2003; image by Gould 1852), and fishes (Oberdorff *et al.* 2019, Jézéquel *et al.* 2020; image by Castelnau 1855). Note that the number of fish species corresponds to the whole basin, but most of them (>95%) are from the lower basin (Albert *et al.* 2011, 2020; Dagosta and de Pinna 2020).

Figure 2.3 A small sample of Amazonian biodiversity. First column: Wire-tailed manakin (*Pipra filicauda*), Amazonian Royal Flycatcher (*Onychorhynchus coronatus*). Second column: Amazon Flying Fish (*Thoracocharax stellatus*), Red Bellied Piranha (*Pygocentrus cariba),* Red-spot Killifish (*Trigonectes rubromarginatus*). Third column: Andean Glassfrog (*Hyalinobatrachium pellucidum*), Red Howler Monkey (*Alouatta seniculus*), La Salle's Shadow-Snake (*Synophis lasallei*). Fourth column: *Columellia oblonga,* Quinine (*Cinchona officinalis*), Red Passion Flower (*Passiflora manicata*). Photos by Camila Ribas and Tomaz Melo (first column), James Albert (second column), Tropical Herping (third column), and Carmen Ulloa Ulloa (fourth column).

mistakenly treated as a single species (Albert *et al.* 2020b).

To fill this gap, integrated studies of Amazonian taxa conducted over the past two decades have employed a combination of molecular and morphological tools that allowed recognition of numerous cryptic species of plants (Damasco *et al.* 2019; Carvalho Francisco and Lohmann 2020), birds (Ribas *et al.* 2012; Whitney and Haft 2013; Thom and Aleixo 2015; Schultz *et al.* 2017, 2019), amphibians (Gehara *et al.* 2014; Jaramillo *et al.* 2020; Vacher *et al.* 2020), fishes (Melo *et al.* 2016; Craig *et al.* 2017; García-Melo *et al.* 2019), and primates (Lynch Alfaro *et al.* 2015). Between 1999 and 2015 alone, many new species of plants (1,155 spp.), fishes (468 spp.), amphibians (321 spp.), reptiles (112 spp.), birds (79 spp.), and mammals (65 spp.) were described throughout the Amazon Basin (WWF 2016).

Spectacular Amazonian species keep being described. They include, for instance, a new critically endangered titi monkey (*Plecturocebus grovesi*; Byrne *et al.* 2016), 15 new species of Amazonian birds described in a single publication (Whitney and Haft 2013); 44 new species of lungless *Bolitoglossa* salamanders that await formal descriptions (Jaramillo *et al.* 2020), a distinctive new and Critically Endangered vanilla orchid (*Vanilla denshikoira;* Flanagan *et al.* 2018), and a new worm-like fish species (*Tarumania walkerae*) that inhabits moist leaf litter deep within the rainforest, and which represents an entirely new family, the Tarumaniidae (de Pinna *et al.* 2018).

Comprehensive knowledge of the species that inhabit hyperdiverse Amazonian ecosystems is central to better understanding their ecosystem functions (Malhi *et al.* 2008) and the emergent properties that arise from non-linear interactions among Amazonian species and their abiotic environments. For example, while it is clear that the Amazon's hydrological cycles depend on forest transpiration, and that they impact climate at a continental scale, the influence of local species and their traits on precipitation patterns and climate remains to be understood (Chambers *et al.* 2007). Large-scale approaches aiming at quantifying unknown biodiversity, such as metagenomics, are also contributing for a deeper understanding of poorly studied life forms (e.g., bacteria, fungi, microorganisms) and ecosystem-level biochemical processes in Amazonian soils (Ritter *et al.* 2020) and rivers (Ghai *et al.* 2011; Santos *et al.* 2019). While still under-utilized, these approaches are revolutionizing our understanding of Amazonian biodiversity patterns and the processes that contribute to them, guiding conservation prioritization approaches and management plans for the basin.

Knowledge of Amazonian biodiversity is crucial to understanding the history of diversification of Amazonian biota, especially the more recent speciation events (Rull 2011). Until recently, a fragmentary knowledge of Amazonian biodiversity at finer taxonomic levels led scientists to use more inclusive taxonomic categories (e.g., genera, families) to understand diversification patterns in this region (Antonelli *et al.* 2009). While these categories provide important insights into overall diversity patterns (Terborgh and Andresen 1998), they cannot be objectively defined, nor compared across taxa, rendering generalizations difficult (Cracraft *et al.* 2020). Integrative approaches that combine standardized field sampling, DNA barcoding (García-Melo *et al.* 2019; Vacher *et al.* 2020), comparative phylogenomics (Alda *et al.* 2019; Santos *et al.* 2019), and artificial intelligence (Draper *et al.* 2020) have accelerated the fine-scale documentation of Amazonian biodiversity (Ritter *et al.* 2020; Vacher *et al.* 2020). These approaches involve new sampling efforts while also relying on museum specimens, which significantly leverage taxonomic work (e.g., Thom *et al.* 2020; Vacher *et al.* 2020). Unfortunately, Amazonian museum collections are still undervalued despite offering a rich source of information (Escobar 2018); local institutions need support to hire experts in the field, and to maintain and expand their biological collections (Fontaine *et al.* 2012; Funk 2018). Human resources and infrastructure support are also crucial for the maintenance of the large databases of Amazonian species compiled to date; while important and useful, they should be constantly vetted and updated to address knowledge gaps and misidentifications.

2.3 Evolution of Amazonian Forests

Flowering plants constitute the main physical structure of Amazonian rainforests. They exhibit a wide variety of growth forms, including woody trees, shrubs, and lianas, as well as epiphytes, herbaceous sedges, grasses, and colonial bamboos (Rowe and Speck 2005). DNA studies suggest that this group of plants first diversified in the Lower Cretaceous (ca. 145–100 Ma) (Magallón *et al.* 2015), but fossil data suggest that flowering plants did not dominate Neotropical ecosystems until the Upper Cretaceous (ca. 100–66 Ma; Hoorn *et al.* 1995; Dino *et al.* 1999; Mejia-Velasquez *et al.* 2012; Carvalho *et al.* 2021).

While some Amazonian organisms have ancient origins, dating back to the early Cenozoic or Cretaceous (Cracraft *et al.* 2020), most species that currently inhabit the Amazon originated within the past few million years (Da Silva *et al.* 2005; Rull 2008, 2011, 2020; Santos *et al.* 2019). The wide distribution of evolutionary ages of Amazonian species suggests that the formation of its modern-day biodiversity took place over an immense time span (Cracraft *et al.* 2020), being influenced by the many changes in the physical landscape during this period (Antonelli *et al.* 2009).

The Amazon was substantially modified by a sudden mass extinction triggered by the impact of a large asteroid or comet about 66 million years ago at the Cretaceous–Paleogene [K-Pg] boundary (De La Parra *et al.* 2008; Carvalho *et al.* 2021; Jacobs and Currano 2021). Many groups of Neotropical birds (Claramunt and Cracraft 2015; Oliveros *et al.* 2019), butterflies (Espeland *et al.* 2015, 2018; Seraphim *et al.* 2018), and fishes (Friedman 2010; Hughes *et al.* 2018) diversified rapidly following this event. Plant communities similar to those seen in today's Neotropical rainforests, although with fewer species, evolved in the Paleocene (ca. 66–56 Ma) (Wing *et al.* 2009; Jaramillo *et al.* 2010a), with many plant lineages diversifying in the Eocene (ca. 56–34 Ma) (Lohmann *et al.* 2013). Indeed, Neotropical rainforest plants seem to have reached a pinnacle of diversity only during the Eocene (ca. 56 Ma), when the wet climates of the Mesozoic still predominated. Eocene forests are thought to have been highly rich in species (Burnham and Graham 1999; Jaramillo *et al.* 2006, 2010a, b). Conspicuous elements of Paleocene Neotropical rainforests include members of key plant families such as palms, herbs (e.g., Araceae, Zingiberaceae), shrubs (e.g., Malvaceae), lianas (e.g., Menispermaceae), and trees (*e.g.,* Lauraceae) (Burnham and Johnson 2004; Wing *et al.* 2009; Carvalho *et al.* 2011).

The drier seasons and cooler climates of the early Oligocene (ca. 30 Ma) contributed to extensive vegetational changes throughout South America. Namely, the once continuous and broadly distributed wet South American rainforests were divided in two, the Amazon and Atlantic rainforests, due to expansion of open subtropical woodland forests in central South America and the establishment of the Seasonally Dry Diagonal (Bigarella 1975; Costa 2003; Orme 2007; Fouquet *et al.* 2012; Sobral-Souza *et al.* 2015; Thode *et al.* 2019). These vegetational changes coincided with the beginning of the uplift of the Mantiqueira Mountains of eastern Brazil and the Northern Andes, causing substantial changes in South American air currents (see Chapter 1). Increasingly drier climates and the expansion of open savannah vegetation types were accompanied by substantial changes in species composition (e.g., palms), the origin of C4 grasses (Vicentini *et al.* 2008; Urban *et al.* 2010; Bouchenak-Khelladi *et al.* 2014), and the expansion of grasslands and open woodlands at the expense of closed-canopy forested habitats (Edwards and Smith 2010; Edwards *et al.* 2010; Kirschner and Hoorn 2020).

In the Miocene, uplift of the Northern Andes led to a profound reorganization of the river network and the formation of the Pebas mega-wetland, a system (Hoorn *et al.* 1995, 2010, 2017; Albert *et al.* 2018), of vast lacustrine and swampy environments in the western Amazon (Hoorn 1993; Wesselingh and Salo 2006). Progressive uplift of the Northern Andes also affected the regional climate, leading to increased precipitation due to the orography (Poulsen *et al.* 2010). Vast areas of flooded forests were then established, composed of palms (i.e., *Grimsdalea*), ferns, and Poaceae, among others (Hoorn 1994; Jaramillo *et al.* 2017; Hoorn *et al.* 2017; Kirschner and Hoorn 2020). In addition, marine incursions into the western Amazon allowed estuarine taxa to colonize the Pebas shores (Hoorn 1993; Boonstra *et al.* 2015; Jaramillo *et al.* 2017).

In the Late Miocene and Pliocene, a major landscape reshaping took place, caused by overfilling of sedimentary basins in the western Amazon with Andean-derived sediments. This led to a renewed drainage reorganization and the onset of the modern transcontinental Amazon River (see Chapter 1). The former Pebas wetland surfaces were colonized by many different lineages (Antonelli *et al.* 2009; Roncal *et al.* 2013), in a process of upland forest expansion that is suggested to have continued until the Late Pleistocene (Pupim *et al.* 2019). Landscape changes also led to increased diversification of numerous plant lineages, such as the flowering plant genera *Inga* (Legumes; Richardson *et al.* 2001) and *Guatteria* (Annonaceae; Erkens *et al.* 2007). At around the same time, the Andean slopes were colonized by many plant lineages, including species of the Malvaceae (Hoorn *et al.* 2019), Arecaceae (i.e., palms; Bacon *et al.* 2018), and Chloranthaceae families (i.e., *Hedyosmum*; Martínez *et al.* 2013). From the Late Miocene to the Pliocene (ca. 11-4 Ma), the rise of the Eastern Cordillera of the Colombian Andes completed the isolation of the *cis*-Andean (Orinoco-Amazon) from the *trans*-Andean (Pacific slope, Magdalena, and Maracaibo) basins, resulting in the isolation of their resident aquatic biotas. Evidence suggests that high levels of plant species diversity existed during the Miocene thanks to a combination of low seasonality, high precipitation, and edaphic heterogeneous substrate (Jaramillo *et al.* 2010a).

The Neogene uplift of the Northern Andes (ca. 23–2.6 Ma; see Chapter 1) had profound effects on Amazonian landscapes, impacting the diversification of both lowland and highland lineages (Hoorn *et al.* 2010; Albert *et al.* 2011b; Givnish *et al.* 2016; Rahbek *et al.* 2019; Montes *et al.* 2021). Yet, despite its importance for biogeography, the specific role of mountain ranges as a dispersal barrier between South and Central American lowland plant lineages is still poorly understood (Pérez-Escobar *et al.* 2017). Different diversification patterns have been detected within and between upland and lowland groups, with higher species richness in lowlands and higher species endemism in uplands. The uplift of the northern Andes and its associated dynamic climate history were key drivers of the rapid radiation of Andean-centered plants (Gentry 1982; Jost 2004; Madriñán *et al.* 2013; Luebert and Weigend 2014; Lagomarsino *et al.* 2016; Vargas *et al.* 2017) and animals (Albert *et al.* 2018; Rahbek *et al.* 2019; Perrigo *et al.* 2020). Near mountain tops, plants of the páramo ecosystem underwent one of the highest speciation rates ever recorded (Madriñán *et al.* 2013; Padilla-González *et al.* 2017; Pouchon *et al.* 2018).

During the Quaternary (last 2.6 Ma), global climate cooling in combination with geomorphological processes strongly altered the western Amazonian landscape. Alluvial megafans (large sediment aprons >10,000 km^2) extended from the Andes into the Amazon (e.g., Räsänen *et al.* 1990, 1992; Wilkinson *et al.* 2010), and floodplains varied in size according to changes in precipitation patterns (Pupim *et al.* 2019). The effect of these cyclic climatic changes on landscape and vegetation composition is yet to be fully understood. Direct studies of the sedimentary and fossil records (Jaramillo *et al.* 2017; Hoorn *et al.* 2017; Mason *et al.* 2019), as well as climatic models (Arruda *et al.* 2017; Costa *et al.* 2017; Häggi *et al.* 2017), suggest that general patterns of regional vegetation cover (i.e. forest, savannah) were relatively more stable in tropical South America than in other regions of the world over the past 100,000 years, but varied spatially and over time under the influence of both geological and climatic changes (Hoorn *et al.* 2010; Antoine *et al.* 2016; Wang *et al.* 2017). The dynamic nature of Amazonian vegetation cover during the Quaternary may not have been extremely drastic (e.g., rapidly replacing closed canopy forest by savanna), but sufficient to change the forest cover and to affect the distribution of specialized species (Arruda *et al.* 2017; Wang *et al.* 2017; Silva *et al.* 2019; but see Sato *et al.* 2021).

Current data fail to support one of the better-known hypotheses for Amazonian diversification, the Pleistocene Refugia hypothesis as originally proposed by Haffer (1969). The Refugia hypothesis proposed that Pleistocene climatic oscillations led to the cyclic replacement of forest- and savanna-covered landscapes, resulting in recurrent isolation and merging of populations, and leading to an increased rate of formation of new species. Extensive data from multiple sources now indicate that savannah and open grassland ecosystems have never been widespread in the Amazon (Liu and Colinvaux 1985; Colinvaux *et al.* 2000; Bush and Oliveira 2006), although the eastern Amazon probably experienced substantial changes in vegetation structure, with possible episodes of open vegetation expansion (Cowling *et al.* 2001; Arruda *et al.* 2017, Sato *et al.* 2021). Further, DNA studies of many groups of plants and animals show relatively constant rates of diversification over many millions of years, without abrupt increases in speciation during the Pleistocene (Rangel *et al.* 2018; Rull and Carnaval 2020). Moreover, direct evidence from the fossil record indicates that many Amazonian plant and animal genera originated long before the Pleistocene (Jaramillo *et al.* 2010a; López-Fernández and Albert 2011; LaPolla *et al.* 2013), and that many fossil Amazonian paleo-biotas were composed of modern genera by the Miocene (c. 22–5 Ma), including grasses (Kirschner and Hoorn 2020), turtles and crocodiles (Riff *et al.* 2010), and fishes (Lundberg *et al.* 2009). Nevertheless, the effects of Pleistocene climate oscillations on the diversification of Amazonian biotas are still incompletely understood, and studies on the evolutionary history of Amazonian vegetation are crucial for improving models forecasting the effects of future Anthropogenic climate change (Brown *et al.* 2016).

2.4 Assembling Megadiverse Amazonian Biota

2.4.1 Diversification Dynamics

Amazonian biodiversity was assembled through a unique and unrepeatable combination of processes that intermingle geological, climatic, and biological factors across broad spatial and temporal scales, involving taxa distributed across the whole of the South American continent and evolving over a period of tens of millions of years (Figure 2.4). From a macroevolutionary perspective, the number of species in a geographic region may be modelled as a balance between rates of speciation and immigration that increase overall species numbers, and extinction that decreases species richness (Voelker *et al.* 2013; Castroviejo-Fisher *et al.* 2014; Roxo *et al.* 2014). A region that accrues high species richness due to elevated speciation rates has been referred to as an "evolutionary cradle" of diversity, i.e., a place of high species origination (Gross 2019). By contrast, a region where species tend to accumulate through low rates of extinction may be called an "evolutionary museum" of diversity (Stebbins 1974; Stenseth 1984). Although a useful heuristic in some contexts, this model is a poor fit to Amazonian biodiversity. Amazonian species and higher taxa exhibit a broad range of evolutionary ages, such that the Amazon serves simultaneously as both an evolutionary cradle and museum. Still, groups with different average phylogenetic ages tend to inhabit different geographic portions of the Amazon basin. Species assemblages in the upland Guianas and Brazilian Shields (>250 – 300 m elevation) often include a mix of both older and younger lineages, while the lowland sedimentary basins often harbor younger lineages. This pattern is observed in many taxonomic groups (e.g., plants, Ulloa Ulloa and Neill 2006; Amazonian rocket frogs *Allobates*, see Figure 2.6, Réjaud *et al.* 2020; fishes, Albert *et al.* 2020a), although exceptions also exist (Castroviejo-Fisher *et al.* 2014; Bonaccorso and Guayasamin 2013). Similar contrasting core-periphery patterns are observed in many Neotropical taxa, including birds, mammals, snakes, frogs, and plants (Antonelli *et al.* 2018; Azevedo *et al.* 2020; Vasconcelos *et al.* 2020). Diversification in response to geographic barriers is one of the most widespread processes that facilitates speciation. In the Amazon, this process is thought to have played an important role in the evolution of the local biota. Geographic barriers can isolate individuals that once belonged to a continuous population of a given species into two (or more) non-overlapping sets of populations (Coyne and Orr 2004). When this geographic separation is maintained for long periods of time, new species may be formed through a process called allopatric speciation (Figures 2.5, 2.6, 2.7). For instance, the uplift of the Andes separated previously connected lowland taxa, preventing dispersal, and establishing new habitats that have fostered the evolution of novel, independent lineages (Albert *et al.* 2006; Hutter *et al.* 2013; Canal *et al.* 2019). This event fragmented the aquatic fauna of northwestern South America, leaving a clear signal on all major taxa (Albert *et al.* 2006). Among families of freshwater fishes, species diversity is significantly correlated with a minimum number of cis-/trans-Andean clades, which indicates that the relative species diversity and biogeographic distributions of Amazonian fishes were effectively modern by the Late Miocene (Albert *et al.* 2006).

Changes in river drainage networks have also strongly affected dispersal, gene flow, and biotic diversification within the Amazon (Figure 2.7). Large lowland Amazonian rivers represent important geographic barriers for groups of primates (e.g., Wallace 1852; Ayres and Clutton-Brock 1992), birds (Ribas *et al.* 2012; Silva *et al.* 2019), fishes (Albert *et al.* 2011a), butterflies (Brower 1996; Rosser *et al.* 2021), wasps (Menezes *et al.* 2020), and plants (Nazareno *et al.* 2017, 2019a, b, 2021). Similarly, past climatic change is believed to have cyclically changed the distribution of Amazonian habitats such as closed-canopy forests, open forests, non-forest vegetation, and cold-adapted forests, often causing population fragmentation and speciation (Cheng *et al.* 2013; Arruda *et al.* 2017; Wang *et al.* 2017; Silva *et al.* 2019).

Apart from the importance of past geographic isolation and speciation due to habitat discontinuity, adaptation to specific habitats has also contributed significantly to species diversification in this region. The large geographical extension of the Amazon, tied to its diverse soil types, provided multiple opportunities for ecological specialization (Box 2.1; Fine *et al.* 2005; Tuomisto *et al.* 2019). This soil heterogeneity reflects the complex geological history of northern South America (see Chapter 1, section 1.4.1).

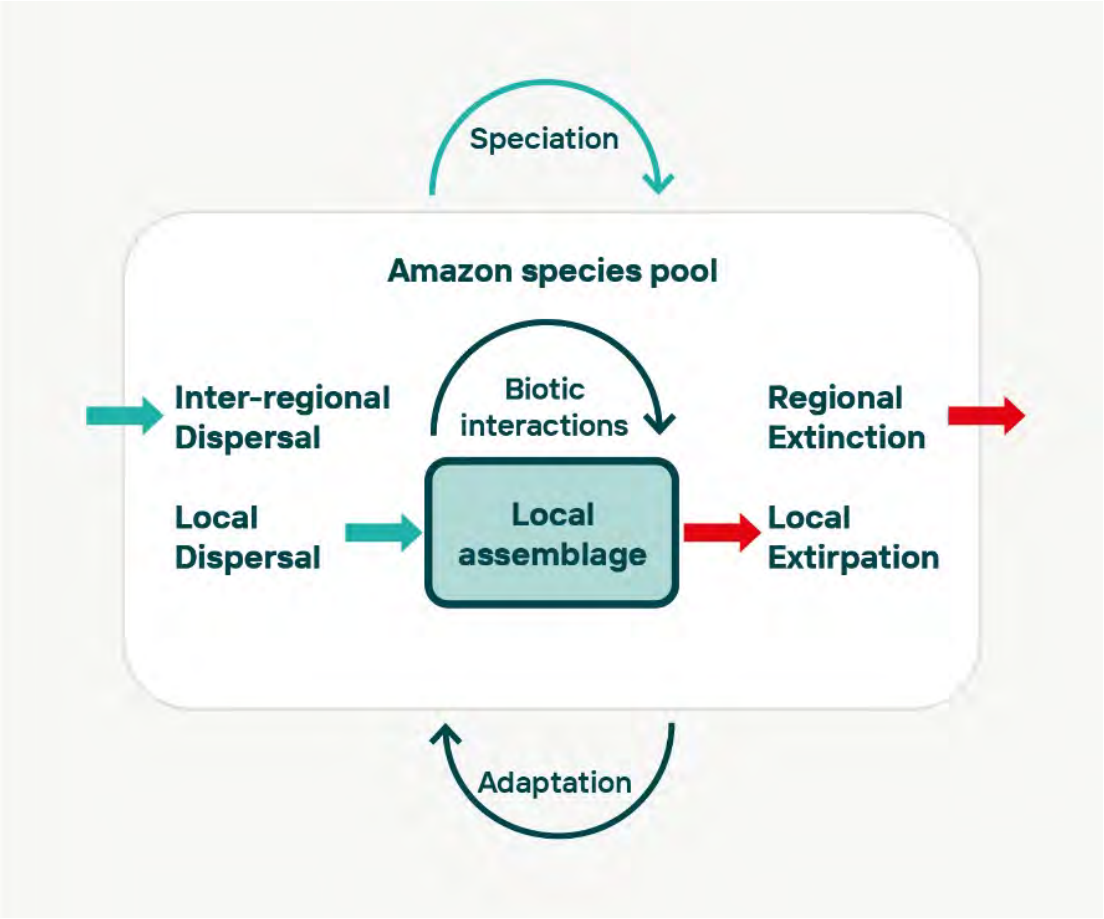


Figure 2.4 Regional and local processes underlying the assembly of the Amazonian biota. The regional species pool (outer light-blue box) is defined as the sum of all the local species assemblages (inner dark-blue box). Blue arrows indicate processes that increase species richness, red arrows highlight those that reduce species richness, green arrows represent processes that modify or filter species traits. Speciation and dispersal contribute new species to the regional pool, while extinction removes species. Habitat filtering, dispersal ability, and facilitation affect the richness of local assemblages by limiting or enhancing the establishment of species pre-adapted to local conditions. Local extinction may arise from biotic interactions (such as predation and competition), or abiotic factors (e.g., tectonics or climate change). Adapted from Ricklefs and Schluter (1993), Vellend and Orrock (2009) and Antonelli *et al.* (2018).

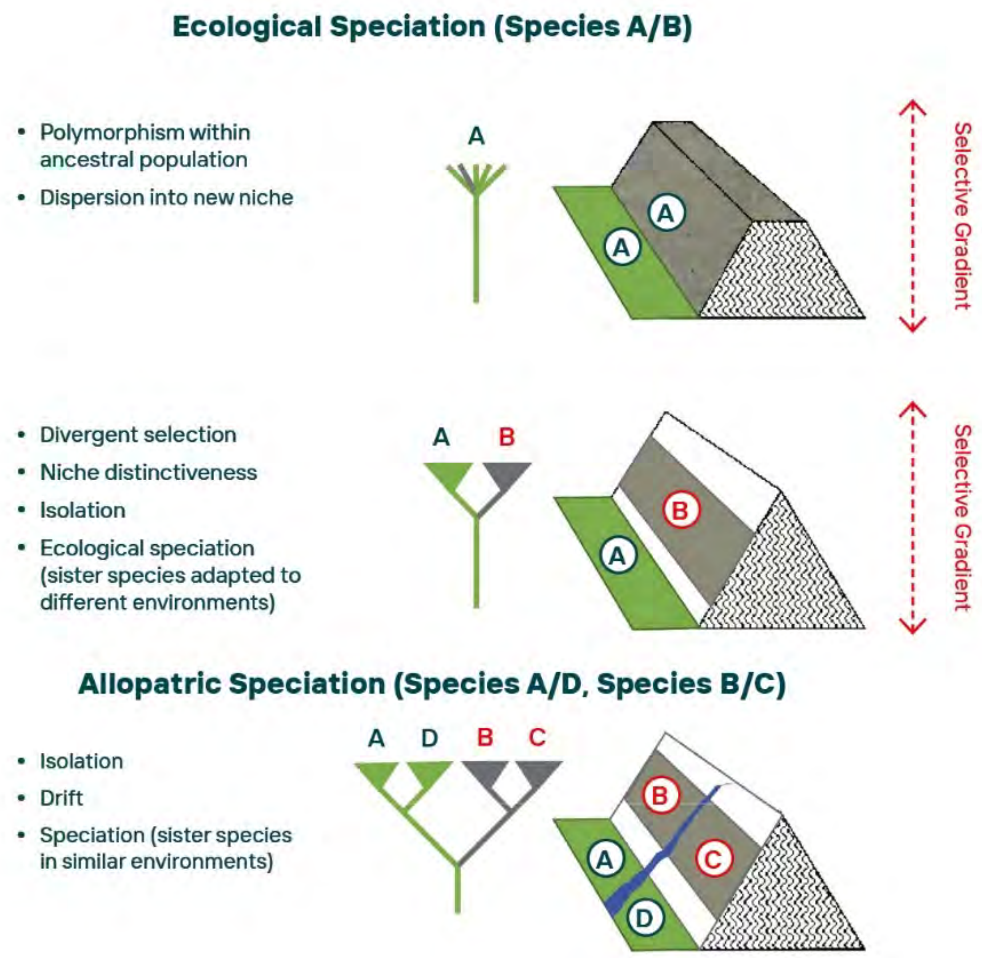


Figure 2.5 Common speciation mechanisms in the Amazon and elsewhere. Ecological speciation: the process by which new species form as a consequence of selection along climatic or ecological gradients, such as those encountered in the Andes. Note that the resulting species occupy distinct environments. Allopatric speciation: when populations of the same species become isolated because of geographical barriers, such as rivers or mountain ranges; note that the resulting sister species occupy the same environment. Modified from Guayasamin *et al.* (2020).

Box 2.1 Adaptations in Amazonian Species

Amazonian plants have evolved multiple adaptations to local conditions. Species of the family Burseraceae (in the genera *Protium*, *Crepidospermum*, and *Tetragastris*) provide classic examples of specialization to the different types of soil that occur throughout *terra firme* (white-sand, clay, and terrace soils) (Figure B2.1.1). In a 2000 km stretch in the western Amazon, 26 of the 35 plant species are associated with only one of the three soil types available; no species is associated with all three habitats. When this pattern of specialization is analyzed together with the evolutionary history of the group, inferred through DNA analyses, it becomes apparent that an association with terrace soils was likely ancestral in this group. Subsequent adaptation allowed some of these plants to occupy white-sand and clay soils. These evolutionary reconstructions also indicate that multiple transitions to clay soil coincide, in time, with the emergence of wide patches of clay soils caused by Andean uplift in the Miocene (Fine *et al.* 2005). In a contrasting example, Amazonian bird species that occur exclusively in patches of white sand vegetation are often related to species from open habitats outside Amazonia, like the Cerrado and Tepuis (Capurucho *et al.* 2020; Ritter *et al.* 2020), and do not have close relatives occupying the adjacent humid forest. This result suggests that the adaptations necessary to occupy these open vegetation habitats may not be common within forest specialized groups.

Figure B2.1.1. Plants and bird species adapt to habitats with different soils. (A) Clay-soil forest. (B) Terrace-soil forest. (C) White-sand vegetation. Photos by Camila Ribas.

While the erosion of the Guiana and Brazilian shields produced the soils of the eastern Amazon, younger sediments that are products of Andean Orogeny have developed soils in the western Amazon that tend to be more fertile. This east to-west gradient in soil fertility is paralleled by a gradient in species composition, wood density, seed mass, and wood productivity (but not forest biomass, see Ter Steege *et al.* 2006; Tuomisto *et al.* 2014). Likewise, different levels of forest inundation during

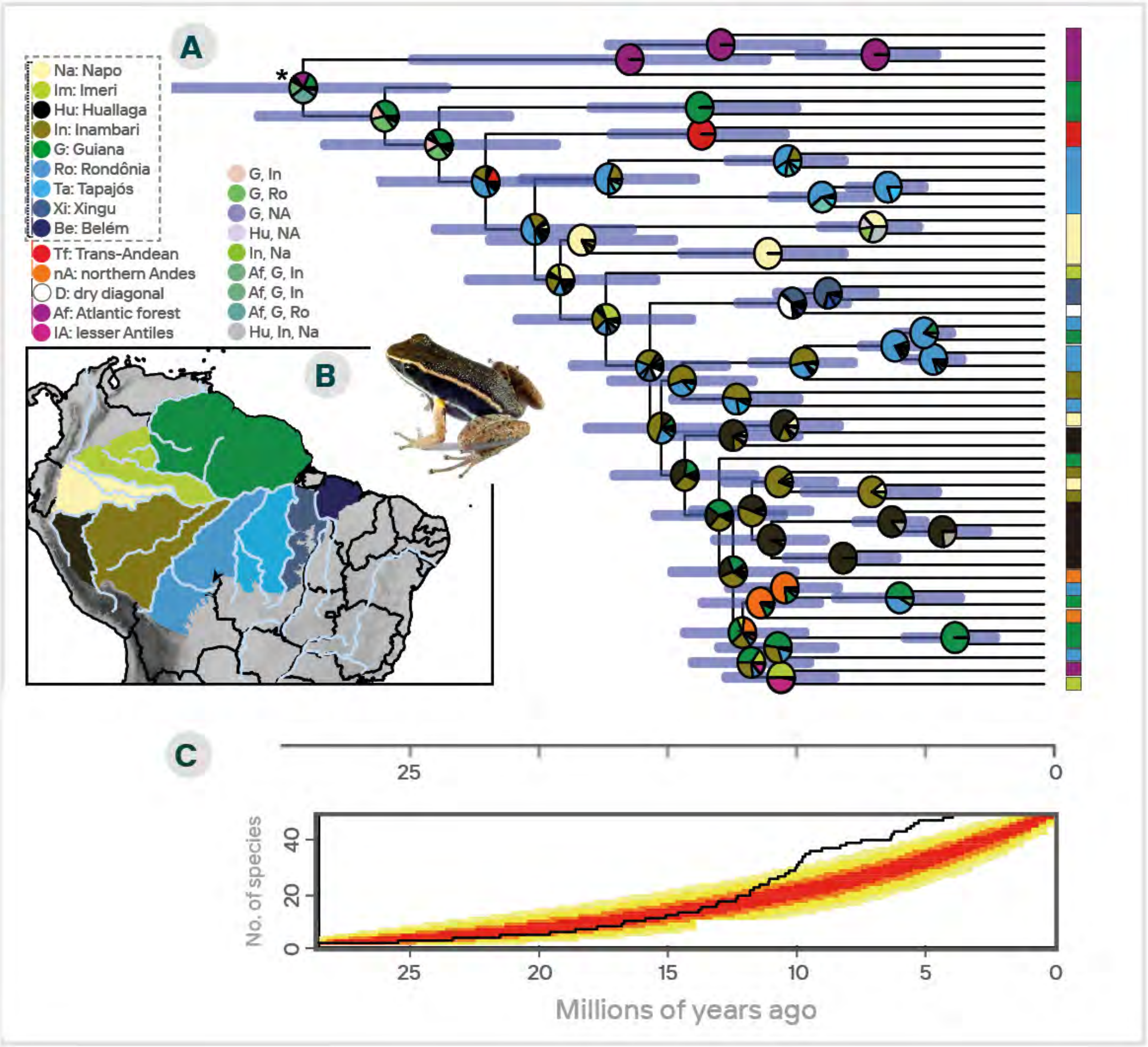


Figure 2.6 Diversification and endemism in Amazonian rocket frogs (*Allobates* spp.). Closely related species display an allopatric pattern of distribution, matching interfluves delimited by modern Amazonian rivers. (A) Evolutionary relationships, represented as a phylogenetic tree. Time is provided along the horizontal axis; blue bars denote the confidence intervals around the inferred time of speciation; pie charts indicate how probable are the estimated ancestral areas of each clade, colored squares represent the current distribution of each species. (B) Amazonian areas of endemism. (C) Inferred number of lineages accumulated through time. Modified from Réjaud *et al.* (2020).

the annual flooding cycle have contributed to the forma-tion of diverse habitat types and specializations in groups of birds and fishes (Albert *et al.* 2011a; Wittmann *et al.* 2013; Luize *et al.* 2018; Thom *et al.* 2020; see also Chapter 1, section 1.5.1).

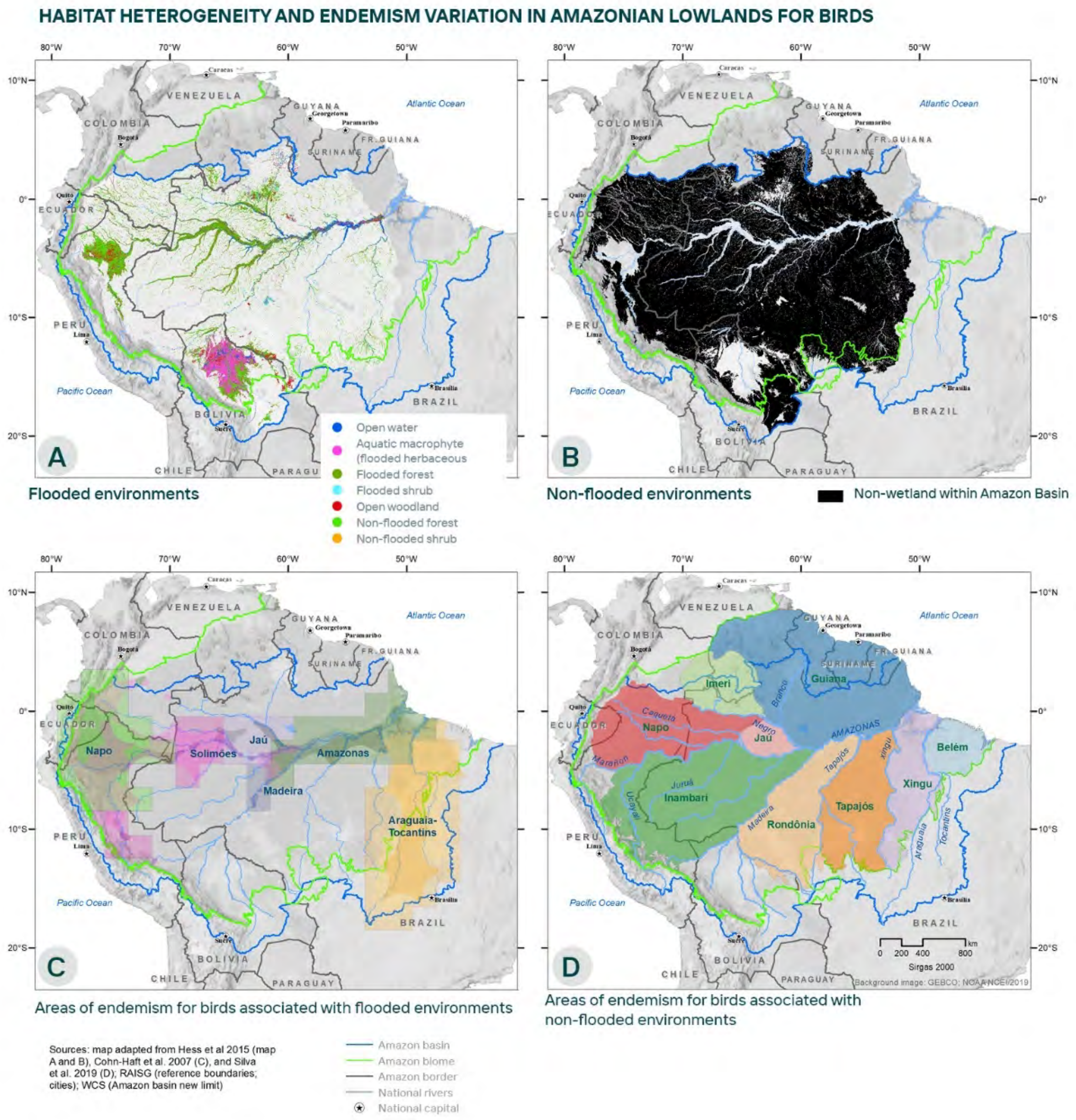
Habitat heterogeneity has played an important role in the formation of Amazonian biodiversity, with geological changes also impacting the ecological conditions available to the Amazonian biota. Andean uplift, for instance, has had a major effect on the Neotropical climate; it created both habitat and climate heterogeneity while leading to the humidification of Amazonian lowlands and the aridification of Patagonia (Blisniuk *et al.* 2005; Rohrmann *et al.* 2016). The Andes, with an average elevation of 4,000 m, exhibit an immense gradient of humidity and temperature. This has provided numerous opportunities for colonization, adaptation, and speciation events in lowland species, such as frogs, birds, and plants, at different times (Ribas *et al.* 2007; Hutter *et al.* 2013; Hoorn *et al.* 2019; Cadena *et al.* 2020a).

As a consequence, the Andes are disproportionately more biodiverse relative to their surface area (e.g., Testo *et al.* 2019); this dynamic interaction between lowlands and adjacent mountains are known to generate diversity worldwide (Quintero and Jetz 2018; Rahbek *et al.* 2019). Repeated cycles of ecological connectivity and spatial isolation in the high Andes (as observed in today's páramos) may have acted as a "species pump" and significantly increased speciation rates in high-elevation Andean taxa due to the joint action of allopatry, natural selection, and adaptation (Madriñán *et al.* 2013; Rangel *et al.* 2018; Pouchon *et al.* 2018).

The contributing roles of abiotic and biotic processes in biodiversification have been neatly summarized as the so-called Court Jester and Red Queen perspectives, respectively (Benton 2009). The Court Jester hypothesis emphasizes the role of abiotic forces as major drivers of speciation (emphasizing, for example, the role of adaptation to climate, substrate, or water condition; Barnoski 2001). Abiotic factors deriving directly from geographic space, climatic and elevation gradients, topographic relief, hydrology, and sediment and water chemistry all serve to facilitate organismal diversification into major habitat types. Intertwined with these landscape processes are innumerable biotic processes that create new species and prevent extinction; e.g., competition, predation, parasitism, mutualism, and cooperation. These biotic interactions can lead to the co-evolution of new traits, increase the structural heterogeneity and functional dimensions of habitats, and enhance the genetic and phenotypic diversity of Amazonian ecosystems (Figure 2.4). Together with the evolutionary processes that emerge from them, these biological interactions are emphasized in the Red Queen Hypothesis. As we discuss below, the immense biodiversity of the Amazon results from both abiotic (see 4.2. Geographical connectivity through time) and biotic (see 4.4. How biodiversity generates and maintains biodiversity) factors.

2.4.2 Geographical Connectivity Through Time

The Amazon basin is a highly heterogeneous set of landscapes and riverscapes that form a mosaic of habitat types, often characterized by distinct floras and faunas (e.g., Duellman 1999; Cardoso *et al.* 2017; Tuomisto *et al.* 2019; Albert *et al.* 2020a). Abiotic changes and shifts in the distributions and connections among these different habitats across space and through time drove the accumulation of the impressive number of Amazonian species (Dambros *et al.* 2020). Because organisms differ so widely in their traits (such as their dispersal ability and physiological tolerances), the same landscape conditions that allow for demographic and genetic connections in some groups can reduce connections in others. For example, while large lowland rivers such as the Amazon and the Negro constitute effective barriers to dispersal in upland species of monkeys and birds (representing boundaries between closely related species of those groups; Cracraft 1985), these very same waterways serve as dispersal corridors for riverine and floodplain species of fishes, birds, mammals, and plants



HABITAT HETEROGENEITY AND ENDEMISM VARIATION IN AMAZONIAN LOWLANDS FOR BIRDS

A Flooded environments

B Non-flooded environments

C Areas of endemism for birds associated with flooded environments

D Areas of endemism for birds associated with non-flooded environments

Sources: map adapted from Hess et al 2015 (map A and B), Cohn-Haft et al. 2007 (C), and Silva et al. 2019 (D); RAISG (reference boundaries, cities); WCS (Amazon basin new limit)

Figure 2.7 Habitat heterogeneity and bird distribution and endemism in the Amazonian floodplains. Distribution of (A) flooded (~14% of the total area) and (B) non-flooded environments (modified from Hess *et al.* 2015). Areas of endemism for birds associated with (C) flooded (Cohn-Halt *et al.*, 2007) and (D) non-flooded (Silva *et al.* 2019) environments.

with seeds dispersed by fishes or turtles (e.g., Albert *et al.* 2011b; Parolin *et al.* 2013).

This habitat heterogeneity may be one of the reasons why past landscape changes that promoted the diversification of co-existing lineages in the Amazon resulted in different geographical patterns of species distributions among groups, and different times of speciation (Da Silva *et al.* 2005; Naka and Brumfield 2018; Silva *et al.* 2019). In this heterogeneous and dynamic landscape, the effectiveness of an isolating barrier depends on the biological characteristics of individual species, such as their habitat affinity, their ability to move through the landscape, their tolerance to temperature and precipitation extremes, their generation time, clutch size, and abundance patterns, among other factors (Paz *et al.* 2015; Papadopoulou and Knowles 2016; Capurucho *et al.* 2020). Low dispersal ability, for example, facilitates geographic isolation and genetic differentiation that tend to increase speciation rates (e.g., tropical insects, Polato *et al.* 2018), but also increase the risk of local extinction (Cooper *et al.* 2008). Thermal tolerances, on the other hand, mediate the impacts of climate on diversity maintenance and speciation rates (Janzen 1967); because tropical species experience relatively stable environmental temperatures across their annual cycle, they have evolved more narrow thermal tolerances and reduced dispersal capacities relative to temperate species (Janzen 1967; Shah *et al.* 2017), which promotes speciation. Lowland tropical species also live under temperature conditions close to their thermal maximum, which places them at risk in the face of increased global warming (Colwell *et al.* 2008; Campos *et al.* 2018; Diele-Viegas *et al.* 2018, 2019).

Because Amazonian species have unique evolutionary trajectories and variable environmental requirements, they have been differentially affected by past geological and climatic events. Patterns of historical connectivity among populations that inhabit upland rainforest habitats have been profoundly influenced by the changing courses of major lowland rivers and their associated floodplains over millions of years, and also by prominent topographic and habitat discontinuities, such as patches of rugged terrain, open savannah vegetation, and sandy soils (Capurucho *et al.* 2020; Cracraft *et al.* 2020). As an example, while the relatively narrow and young Rio Branco delimits the distribution of some primate species (Boubli *et al.* 2015), this river has had a dual role in the evolution of some birds (Naka and Brumfield 2018), plants (Nazareno *et al.* 2019a, b, 2021), and some small-bodied fishes (Dagosta and Pinna 2017), serving as an effective barrier for some species but not for others. Ecological traits are hence important not only to define the distribution and degree of connectivity of extant populations, but they have also influenced their evolutionary history over time.

Both terrestrial and aquatic Amazonian habitats have been profoundly affected by climate change, especially changing precipitation patterns and sea levels, over millions of years. Many studies have discussed the influence of past climates on Amazonian landscapes while focusing on changes of the relative cover of forest and savanna (Bush and Oliveira 2006). However, more subtle changes in forest structure may also affect species distributions and landscape connectivity (Cowling *et al.* 2001; Arruda *et al.* 2017). Understanding how to maintain population connectivity is key to protecting Amazonian biodiversity. For instance, it is believed that the resilience of upland Amazonian forest taxa has relied on the historically large dimensions of suitable habitat that allowed them to track appropriate climatic conditions, possibly explaining why so many upland forest species exhibit signs of relatively recent changes in population size (Silva *et al.* 2019). These historical dynamics lay the foundation for predictions of how future climate change will affect patches of humid forests, which are becoming increasingly fragmented due to deforestation and other human land-use activities.

2.4.3 Trait Mediated Diversification in a Heterogeneous Amazon

Studies that consider the habitat affinities of Amazonian species show that the history of each taxon, and its resilience through time, is deeply linked to the kinds of environments it occupies. This view is transforming the way scientists and the general public view the Amazon. Because the heterogeneity of lowland Amazonian habitats has been underappreciated, and because the region has been (wrongly) perceived as a large and homogeneous ecosystem, many taxa have been mistakenly considered widespread and generalist, and, consequently, resilient to landscape change (Bates and Demos 2001). In birds, one of the best studied groups in Amazonia, it has been demonstrated that species from upland non-flooded forest have different ecological associations and evolutionary histories relative to the species that inhabit the floodplains and to those in open vegetation areas (Figure 2.8). Consequently, the geographical distribution of biological diversity differs among those three groups, and so does their resilience to future environmental shifts (Capurucho *et al.* 2020; Cracraft *et al.* 2020; Thom *et al.* 2020). Birds associated with upland non-flooded forest are the most diverse (currently comprising about 1,000 species; Billerman *et al.* 2020). In these groups, distinct species, although closely related, are found in each main Amazonian interfluve (Figure 2.7; Silva *et al.* 2019). Similar patterns have also been described for other groups of Amazonian organisms mostly distributed in upland forests (e.g., Craig *et al.* 2017; Godinho and da Silva 2018).

By contrast, populations associated with seasonally flooded environments, whose available habitats are currently distributed along the main Amazonian rivers, have been impacted by drastic habitat change due to shifts in the drainage system during the last 5 Ma (Bicudo *et al.* 2019), including significant changes even within the last 45 ka (Pupim *et al.* 2019). While large rivers are barriers for the dispersal of small-bodied understory birds in humid non-flooded forests, the seasonally flooded vegetation that grows along these rivers promotes connections across populations of floodplain-associated species adapted to the annual flooding cycle of river floodplains. Differently from the upland non-flooded forest birds, floodplain species have little intraspecific diversity, but they represent older lineages that originated during the Middle to Late Miocene (5–11 Ma; Thom *et al.* 2020). The largest genetic differences within these widespread floodplain species is observed between populations from the western sedimentary basins and populations from the eastern shields (Thom *et al.* 2018, 2020). These distinct evolutionary trajectories have helped to shape the history of Amazonian floodplains (Bicudo *et al.* 2019). Data from floodplain-adapted birds and fishes, for instance, indicate historically larger and more connected populations in the western Amazon (Santos *et al.* 2007; Thom *et al.* 2020), and cycles of connectivity and isolation between species that occupy seasonally flooded habitats in the eastern vs. western Amazon. Organisms adapted to seasonally flooded landscapes are particularly vulnerable to disruptions of connectivity caused either by historical landscape change or to anthropogenic impacts such as dams and waterways (Latrubesse *et al.* 2017; Anderson *et al.* 2018).

Species associated with open vegetation growing on sandy soils have yet a third pattern of diversity distribution in the Amazon. In plants and birds, for instance, populations of the same species are distributed in patches of open habitat separated by upland and flooded forests and located thousands of kilometers apart, spanning all the main interfluvia (Capurucho *et al.* 2020). Despite having a naturally fragmented distribution today, these species were less isolated in the past, suggesting that, although present in the Amazon for millions of years, the distribution of open vegetation has varied through time (Adeney *et al.* 2016).

Together, these contrasting patterns indicate that the Amazonian landscape and its different habitats have been spatially dynamic during the last 10 million years, and that the current distribution of habitats and species represents a snapshot in time.

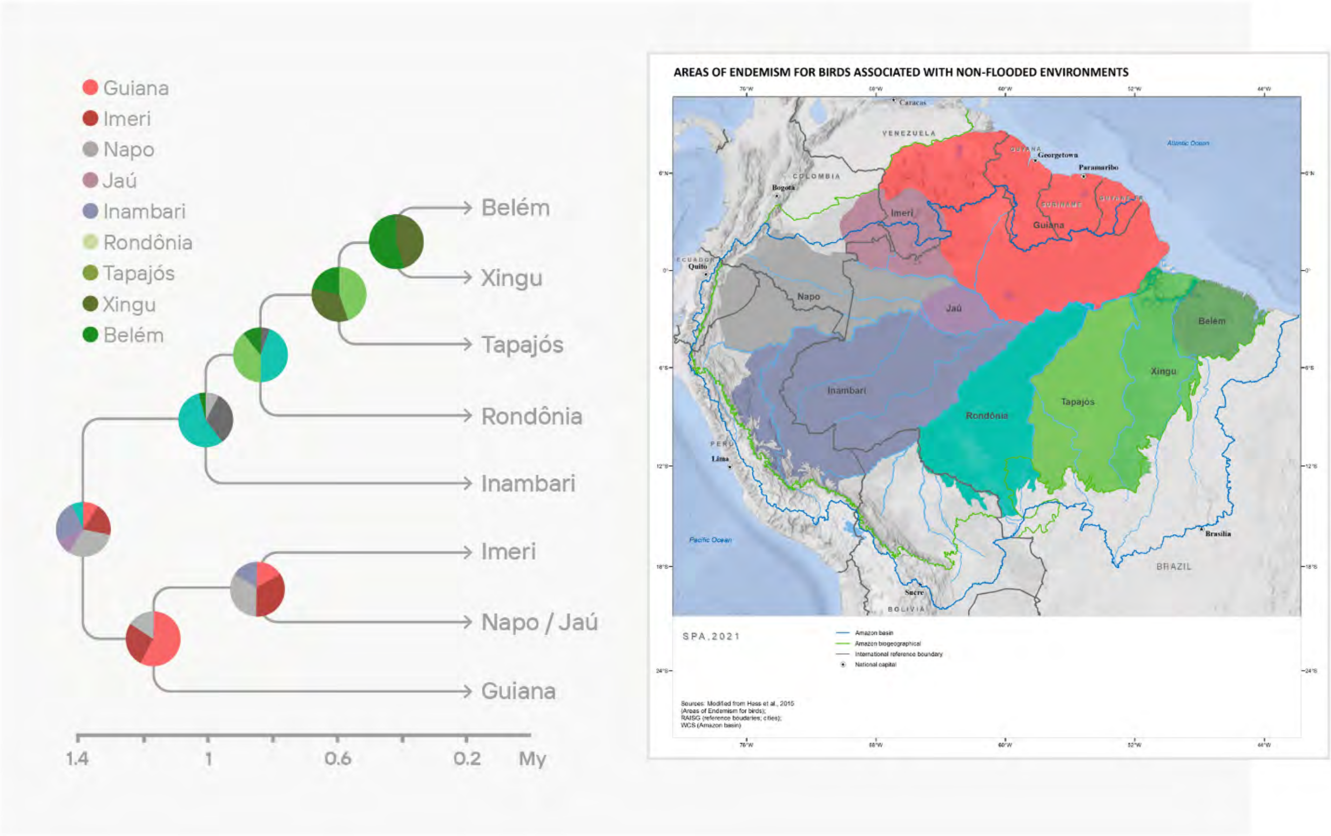


Figure 2.8 Summary of diversification patterns for 21 taxonomic clades of Amazonian birds restricted to the upland forest (*terra firme*) understory. Left: Relationships among nine areas of endemism, inferred from genetic data; pie charts denote ancestral area probabilities. Right: Areas of endemism currently recognized for upland forest birds. Notice how the diversification history of this group matches the location of Amazonian rivers that delimit areas of endemism (e.g., the Rio Tocantins between the Belém and Xingu endemism areas). Also evident is an initial differentiation between clades north of the Amazonas river (represented by the areas Guiana, Imeri, Napo/Jaú) from those south of it (Inambari, Rondonia, Tapajós, Belém, Xingu). Modified from Silva *et al.* (2019).

2.4.4 How Biodiversity Generates and Maintains Biodiversity

There is little doubt that diverse biotas with many functionally distinct organisms, complex biotic environments, and multiple ecological interactions and opportunities facilitate species coexistence and elevate regional species richness and density values. In this regard, biological diversity may be understood to be autocatalytic: species richness itself is a key feature in the origin of hyperdiverse Amazonian ecosystems (Sombroek 2000; Albert *et al.* 2011b; Dáttilo and Dyer 2014).

The notion that biotic interactions help drive organismal diversification is not new. In a famous article, the paleontologist Leigh Van Valen (1973) observed that the life span of species as shown by the fossil record was roughly constant. Borrowing from a line in *Through the Looking Glass* by Lewis Caroll, where the Red Queen tells Alice *"It takes all the running you can do, to keep in the same place"*, he proposed the Red Queen Hypothesis as a metaphor to express the idea that lineages do not increase their ability to survive through geological time (Van Valen, 1973). In modern evolutionary theory, Red Queen dynamics refers to phenotypic evolution in response to biotic interactions, such as the coevolution of parasites and their hosts, chemically defended prey and their predators, and interactions between pollinators and the plant species they visit. In all these biotic interactions, adaptive changes in one species may be followed by adaptations in another species, spurring an evolutionary arms race that may result in co-evolution or extinction, or both.

Other examples of potential Red Queen dynamics include organisms that affect the physical environment that is experienced by other species, such as plants that constitute structural habitat (e.g., tank bromeliads, which provide breeding habitat for frog species and invertebrates), or organisms that modify the physical and chemical environments utilized by several other taxa (e.g., fungi and earthworms that change soil and water chemistry). Organismal interactions such as those, which benefit at least one member of a local species assemblage, are referred to as biotic facilitation. Below, we provide several examples of how biotic interactions have facilitated the evolution of Amazonian diversity.

Host-parasite interactions Because the species composition of many parasite groups often tracks that of their hosts, it is possible to estimate a minimum number of parasite species by comparison to the diversity of their host taxa. Given that many fish parasites exhibit strong host-specificity, it is believed that the actual diversity of the parasites could rival the immense diversity of their fish hosts (Salgado-Maldonado *et al.* 2016). At present, only about 300 species of Neotropical monogenoid flatworms are described, all ectoparasites of fish gills and the external body surface; however, these numbers are rising rapidly due to ongoing taxonomic research; see Vianna and Boeger (2019). Moreover, tight associations between helminth (flatworm and roundworm) and haemosporidian (*Plasmodium*) parasites and host species have been reported in many groups of Amazonian vertebrates, including fishes (Thatcher 2006), amphibians and reptiles (McAllister *et al.* 2010), and birds (Fecchio *et al.* 2018). The diversity of protozoan parasites of vertebrate hosts in the Amazon is presumably much greater still, based on what is known from better-studied faunas (Dobson *et al.* 2008). Even less is known about the diversity of Amazonian insect and plant parasites, but glimpses provided by recent studies using environmental genomics indicate the existence of extraordinary genetic and functional diversity of metazoan and protozoan parasites in the Amazon (Mahé *et al.* 2017; Puckett 2018).

Niche construction Biological diversity also contributes to the evolution of more diversity through the many ways by which organisms modify their external environments. The process by which organismal behaviors alter their local environments is called niche construction, which also affects the ecological conditions for all organisms in a local assemblage (Odling-Smee *et al.* 2013). Organismal behaviors strongly affect and even create many important habitats in the Amazon. These activities include nest-burrow construction and fruit-seed-pollen dispersal by animals, the formation of vegetation structure and shade by plants, and the roles of plants, fungi, and soil or water microbes in nutrient and energy cycling, soil and water chemistry, and fire regimes (Mueller *et al.* 2016; Santos-Júnior *et al.* 2017). Earthworms (*Clitellata*, Annelida) represent a classic example of how niche construction elevates habitat heterogeneity and biodiversity in the Amazon. Earthworms are important ecosystem engineers, whose activities help to mineralize soil organic matter, construct and maintain soil structure, stimulate plant growth, and protect plants from pests (Marichal *et al.* 2017). Several other Amazonian taxa are also important engineers of terrestrial ecosystems, including especially fungi (Palin *et al.* 2011), termites (Duran-Bautista *et al.* 2020), and ants (Folgarait 1998).

Keystone species The high number of fish species in aquatic Amazonian ecosystems can strongly affect nutrient and energy cycling (Winemiller and Jepsen 1998; Arruda *et al.* 2017). A striking example is the ecological role of the “coporo” or “sábalo” (*Prochilodus mariae*), a detritivorous and migratory characiform fish that is functionally important in Andean foothill streams of the western Amazon and Orinoco basins. Selective exclusion of this single species qualitatively changes the structure of local aquatic communities, as measured by sediment accrual and the composition of algal and invertebrate assemblages (Flecker 1996). Another example is provided by planktivorous electric fishes (Gymnotiformes) that constitute the base of aquatic food webs in the Amazon and Orinoco basins (Lundberg *et al.* 1987; Fernandes *et al.* 2004). Because these food webs are essential to support the regional fisheries on which millions of Amazonian people depend as a primary source of animal protein (Goulding *et al.* 2019), planktivorous fishes are a keystone species to human-dominated Amazonian landscapes.

Predator-prey interactions and the evolution of chemical diversity Predator-prey dynamics are one of the most powerful evolutionary forces in nature, resulting in a myriad of strategies and weaponry to prey or avoid predation. Some long-evolved interactions between Amazonian species are responsible for the generation and accumulation of natural products amenable to bioprospection. Amazonian poison frogs (family Dendrobatidae), for instance, are known to sequester chemical defenses from the arthropod prey that they feed upon. These alkaloids (Box 2.2) are used by Indigenous people and explored by the medical community and the pharmaceutical industry (Daly *et al.* 2000; Cordell *et al.* 2001; Philippe and Angenot 2005). Mites, ants, beetles, and millipedes have all been flagged as sources of alkaloids for poison frogs worldwide (Saporito *et al.* 2009; McGugan *et al.* 2016), and several species of frogs are able to further modify them chemically, leading to other alkaloids (Daly *et al.* 2003, 2009). Moreover, although more research is pending, some poison frog alkaloids appear to be derived from plants. This reflects the complex trophic interactions between plants, the arthropods that feed on them, and the frogs that prey on those arthropods (Tokuyama and Daly 1983).

The potential of plants for the Amazonian bioeconomy is enormous. For instance, Amazonian people have known the effects of plant alkaloids as medicine for centuries. Plant alkaloids evolved as a defense mechanism against herbivory (Gauld *et al.* 1992) and are synthesized in the roots, stems (e.g., banisterine), leaves (e.g., caffeine), flowers, fruits, seeds (e.g., strychnine), and bark (e.g., quinine). Some of the most common plant alkaloids include the antimalarial quinine, hunting poisons (barbasco, curare), stimulants (guayusa, nicotine, coca), and ritualistic herbs (ayahuasca, scopolamine). Many of these compounds are precursors for modern medicine; however, due to their complex chemical structures, only a fraction go into commercial production (Reis *et al.* 2019). Moreover, allochemicals from some Amazonian plants might prove useful as sources of biodegradable pesticides; the Piquiá (*Caryocar*), for instance, produces a compound that seems to be toxic to the dreaded leaf-cutter ant (*Atta*), which causes large financial losses to South American agriculture each year (Plotkin 1988). Today, entire companies are dedicated to screening chemical compounds in plants, insects, and frogs, in search for potential drugs. Natural products and their derivatives have been, and continue to be, a primary source in the drug discovery domain (Lopes *et al.* 2019).

2.5 Species Loss and Species Turnover in Amazonia: Lessons from the Fossil Record

Extinctions have occurred many times throughout Earth's history, representing an elemental process contributing to evolutionary diversification. It has been estimated that more than 99% of all species that have ever lived on Earth are now extinct (Raup 1986). The fossil record offers unique evidence to study extinctions; paleontologists have identified 18 time intervals with elevated extinction rates over the past 540 million years, five of which are classified as mass extinction events (Bambach 2006). Models based on DNA analyses and the fossil record, especially of marine invertebrates and mammals, show that background extinction rates over geological time have ranged from 0.02 to 0.14 extinctions per million species per year. In turn, speciation rates are estimated to be about twice this value, ranging from 0.05 to 0.20 speciation events per million species per year (Jablonski 2005; De Vos *et al.* 2015). The fossil record also shows changes in biodiversity over geological time with occasional catastrophic mass extinction events, when extinction rates increased by thousands of times eliminating large clades with distinctive genes and body plans (Bambach 2006; Ceballos *et al.* 2015).

This understanding of the past allows us to put in perspective the wave of extinctions faced by the modern biota, which is estimated to be 1,000 to 10,000 times larger than the background rate, and therefore similar in scope to that of past mass extinction events (Ceballos *et al.* 2015). While its causes are multiple, the increase in the concentration of carbon dioxide in the atmosphere, and the acidification of the oceans caused by human action, match the great natural environmental changes that triggered mass extinction events in the deep past.

BOX 2.2: The Evolution of Jumping Pharmacies: Chemical Defenses of Frogs

Biological diversity is much more than the number of species living in a region. It also encompasses all ecosystem services that species provide. Amazonian frogs, for instance, can be particularly important for the pharmaceutical industry, providing potent alkaloids. In the skin of Neotropical poison dart frogs (family: Dendrobatidae), more than 500 different alkaloids have been reported (Saporito *et al.* 2011). Particularly relevant to bio-prospection are the drivers of alkaloid diversity, which reflect both frog species identity and local environmental conditions, including the local community of prey and abiotic conditions (Daly *et al.* 1992; Saporito *et al.* 2011; McGugan *et al.* 2016). These alkaloids seem to provide chemical defenses against predators, fungi, and perhaps ectoparasites (e.g., Brodie and Tumbarello 1978; Fritz *et al.* 1981; Macfoy *et al.* 2005; Weldon *et al.* 2006). Alkaloid sequestration and modification is both an outcome of biotic interactions between Amazonian frogs and their invertebrate prey, and a mediator of interactions between those same frogs and their predators. Moreover, because a few non-toxic frog species have evolved ways to mimic the coloration patterns of toxic frogs, this predator-prey interaction often expands to impact the survivorship of other local amphibians (Darst *et al.* 2006).

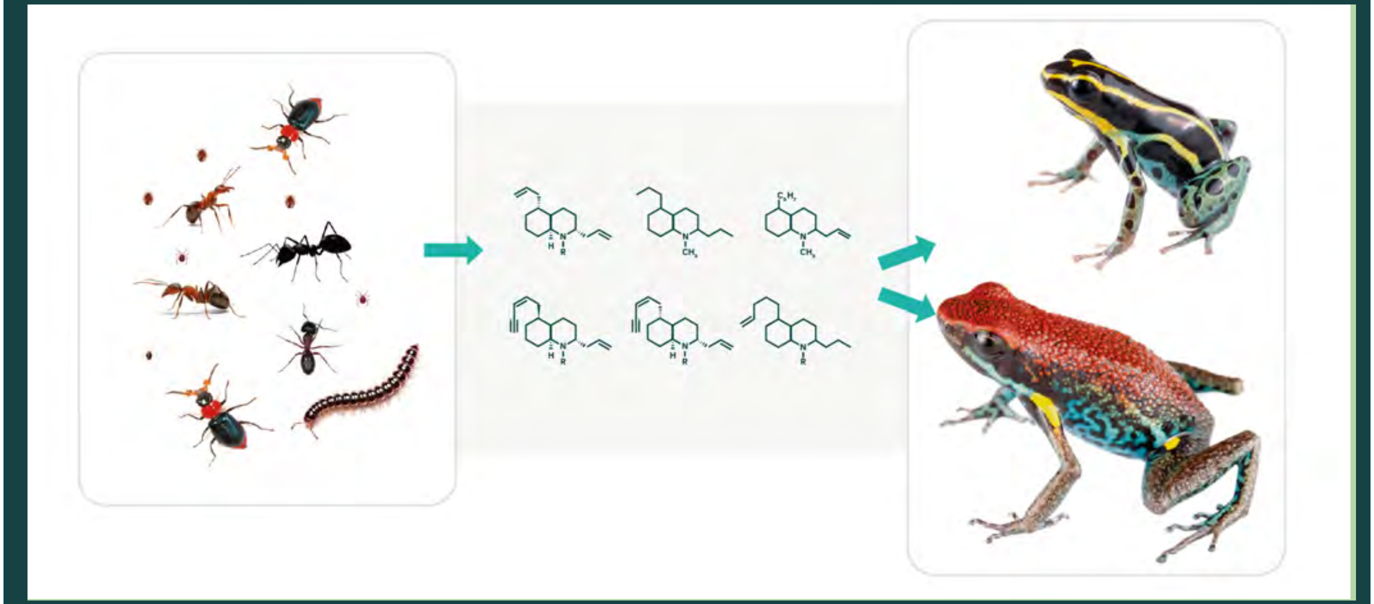


Figure B2.2.1 Poison dart frogs are protected by alkaloids that they sequester from their prey, including ants, mites, millipedes, and melyrid beetles (see Saporito *et al.* 2011 and references therein).

Throughout its lengthy geological history, the Pan-Amazonian region has undergone extensive environmental changes, driven primarily by regional tectonic and global climatic forces. The Pan-Amazon once extended over most of northern South America, with lowlands characterized by alternating fluvial and lacustrine conditions and marginal marine embayments. Modern lineages of Amazonian organisms have survived and adapted to five major rearrangements of landforms and habitats during the Cenozoic (66–0 Ma), as follows:

(i) The Paleogene uplift of the Central Andes, caused by plate subduction along the Pacific margin and the breakup of the Pacific plate (ca. 23 Ma; see Chapter 1), resulted in the establishment of a sub-Andean river basin draining north towards a large embayment of the Caribbean Sea. The basin extended over the area that is now occupied by the Colombian and Venezuelan Llanos.

(ii) Mountain-building in the central and northern Andes narrowed the Caribbean influence and led to the origin and movement of mega-wetlands in the western Amazon ca. 22–10 Ma. The Pebas mega-wetland system resulted from this expansion, reaching more than 1 million km^2 (see Chapter 1).

(iii) Intense Andean mountain building since the late-middle Miocene (last 10 Ma), which coincided with global fluctuations in sea level, prevented further marine influences in the western Amazon and along the northern Andean foreland basin. This retained much of the drainages that flowed into the Pacific and the Caribbean, and formed the wide floodplain named the Acre System.

(iv) From the end of the Miocene (ca. 7 Ma) on, further Andean uplift forced the mega-wetland to be completely drained. This led to the development of widespread river terrace systems with expanded *terra firme* rainforests.

(v) The closure of the Central American Seaway and the emergence of the Panama Isthmus (ca. 15–3.5 Ma) provided opportunities for extensive migrations of North American lineages to both the Amazon and new montane habitats in the Andes.

The biotic responses to these immense environmental changes included dispersal and habitat shifts at the organismal level, adaptation and geographic range shifts at the population level, and speciation and extinction at the species level (Box 2.3).

While the geological record does not provide evidence of sudden mass extinction events during the Cenozoic in the Amazon, some groups of animals once abundant in both terrestrial and aquatic environments were extirpated by one or more of the aforementioned events, including species expected to provide a variety of ecological functions. The fossil record evidences pulses of extinctions between each of the stages are above.

The most significant extinctions were those affecting the rich and endemic lacustrine fauna, notably bivalve mollusks (Wesselingh and Ramos, 2010) and crocodilian reptiles (Riff *et al.* 2010; Scheyer *et al.* 2013; Salas-Gismondi *et al.* 2015). These extinctions occurred in the transition from the lacustrine-fluvial Pebas to the fluvio-lacustrine Acre mega-wetland systems, in association with the origin of the modern transcontinental Amazon River, ca. 9–4.5 Ma (Albert *et al.* 2018).

Mollusks and crocodilians are among the best represented clades in the fossil record of the Amazon. They exemplify the diversification and subsequent extinction of aquatic fauna in association with the evolution of mega-wetlands during the Neogene. About 85 species of mollusks were documented from the last stages of the Pebas System (Middle to Late Miocene). This fauna was dominated by Pachydontinae bivalves, which originated in coastal Pacific and Caribbean marine waters. Marine mollusks colonized the western Amazon during pulses

BOX 2.3: Amazonian Past Diversity and Landscape

The main records about the dawn of the current Amazonian forest are the plant and animal fossils from the Paleocene period (~58 Ma) found in the Cerrejon Formation in northern Colombia (Wing *et al.* 2009). The fossils indicate a high diversity of characteristic tropical plant lineages (e.g., palms and legumes), herbivorous insects (Wing *et al.* 2009) and a unique fauna of giant snakes, crocodiles, and turtles (Head *et al.* 2009). In the past, Amazonia occupied a larger area than today. The Pan-Amazonia included the area of the present Amazon, Magdalena, and Orinoco basins. The fossil faunas of La Venta (13–11 Ma) in the Magdalena valley in Colombia (Kay *et al.* 1997), and from Acre in Brazil and Urumaco in northwestern Venezuela (~11–6 Ma) provide evidence of the past diversity and landscape change in Amazonia through time (Sanchez-Villagra *et al.* 2010). The fauna of La Venta records a high variety of mammals characteristic of tropical forest, such as primates and bats, as well as giant crocodiles and turtles and numerous freshwater fishes (Kay *et al.* 1997). Similarly, the fauna of Acre in Brazil and Urumaco in Venezuela includes a high diversity of mammals, crocodiles, turtles, and fishes (Sanchez-Villagra *et al.* 2010). The fossil record of aquatic vertebrates, such as crocodiles, turtles, and fishes from La Venta and Urumaco, clearly shows that these regions were connected with the current Amazonia, when the Pebas mega wetland existed (e.g., Cadena *et al.* 2020b).

Figure B2.3.1 Past diversity in Amazonia and the mega-wetland landscape. Left: Diversity changes through time, as shown by the fossil record. Notice that floral diversity has remained high since the Paleogene (ca. 60 Ma), and crocodiles and mollusks diversified with the onset of the megawelands and declined with its demise (modified from Hoorn *et al.* 2010). Right: Reconstruction of the Amazonian landscape during the middle to late Miocene (16–7 Ma) highlighting the giant caiman *Purussaurus brasiliensis* preying a *Trigodon* toxodont. Illustration by Orlando Grillo, in Hoorn and Wesselingh (2010).

of marine ingressions ca. 23–15 Ma, together with other aquatic animal groups such as freshwater stingrays, anchovies, needlefishes, dolphins, manatees, and various parasitic lineages (Lovejoy *et al.* 1998). Small, blunt-snouted crocodilians evolved crushing dentitions that allowed them to feed on hard-shelled organisms and prey on the Pebasian malacofauna (Salas-Gismondi *et al.* 2015). The crocodilian fauna of the Pebas system also included species specialized in eating fish (long-snouted gharials), large to giant preys (*Purussaurus*), "gulp-feeding" of small preys (*Mourasuchus*), and generalized small preys (*Caiman* and *Paleosuchus*). On land, the last representatives of an extinct group of terrestrial crocodyliforms, the Sebecidae, competed with mammals as top-predators. This group included the largest terrestrial predator of the Amazon during the Middle Miocene, *Barinasuchus arveloi*, from the Parangula Formation in Venezuela, which reached up to 6 meters in length (Paolillo and Linares 2007). Because top predators are very susceptible to drastic environmental changes, it is likely (although not yet confirmed) that the changes in the mega-wetland impacted the survivorship of these organisms (Salas-Gismondi *et.al.* 2015).

With the end of the Pebas System, most of the associated molluscan fauna became extinct. Consequently, modern Amazonian mollusk diversity is remarkably poor and dominated by cosmopolitan freshwater groups, such as freshwater mussels, clams, and snails (Wesselingh and Ramos 2010). The disappearance of the Pebasian endemic mollusks adversely affected the Pan-Amazonian crocodilians, who then suffered their first large-scale extinction event (Salas-Gismondi *et al.* 2015, Souza-Filho *et al.* 2019).

Still, most of the crocodilian lineages survived to the formation of the Acre System ca. 10–7 million years ago. In the extensive wetlands of the Acre system flourished a notable diversity of around 30 species showing morphological variation greater than any other crocodilian fauna, extant or extinct (Riff *et al.* 2010; Cidade *et al.* 2019). Similarly, the period witnessed a large diversity of turtles, including one of the largest turtles that ever lived on Earth, more than 2.5 m in length and with an estimated body mass of ca. 1,000 kg (Cadena *et al.* 2020b). Beyond some generalist genera that have been present in the Amazon since the Middle Miocene through to today (e.g., *Caiman*, *Melanosuchus*, and *Paleosuchus*), the availability of large-bodied prey and competition with other aquatic predators likely triggered the evolution of giant top predators. Examples include *Purussaurus brasiliensis*, with its 12-meterlong body (Aureliano *et al.* 2015), highly specialized forms such as the bizarre species in the genus *Mourasuchus*, known for their long, wide, dorsoventrally flat skull, and tiny dentition (Cidade *et al.* 2019), and the long-snouted gharials, some also giant in size (Riff *et al.* 2010).

However, the transition from the Acre System to the modern fluvial and *terra firme* Amazonian environments, starting at around 7 Ma, led to a large extinction event affecting crocodilian fauna. All specialized forms, from small to giant, vanished. The extant South American crocodilians are now a small fraction of their former diversity. Entire body types and ecological roles among aquatic fauna disappeared after the demise of the Amazonian Miocene mega-wetlands.

In stark contrast to the turnover of mollusks and crocodilians, modern Amazonia fish fauna have remained largely unchanged at the genus level and above. Direct evidence from the fossil record indicates that all but one fossil genus known from the Miocene is still living (Lundberg *et al.* 1998). Further, molecular phylogenies of most Amazonian fish genera are now available, including more than 1,000 of the 3,000 known species (van der Sleen and Albert 2017). In combination, these datasets indicate that most genera that compose today's rich Amazonian fish fauna were present by the middle Miocene (ca. 15–10 Ma). The evolutionary origins of most Amazonian fish forms and their ecological roles predate the geological assembly of the modern Amazon and Orinoco basins during the Late Miocene and Pliocene (ca. 9–4.5 Ma; Albert *et al.* 2011b).

The tectonics that elevated the Andes and caused the great environmental changes mentioned above also elevated the terrestrial route that ended a long-lasting isolation of South America from other continents during most of the Cenozoic (Croft 2016). This isolation, which led South America to harbor a peculiar and endemic mammalian megafauna (Defler 2019), ceased when the formation of the Isthmus of Panama facilitated the biotic interchange between North and South America, through the event known as the Great American Biotic Interchange (GABI; Stehli and Webb 1985). This connection had great implications for the historical assembly of the Amazonian fauna and flora. Plants, which have a greater dispersal ability, dispersed before animals did, even before a land bridge was fully established between the continents (Cody *et al.* 2010). The fossil record of terrestrial mammals, which is abundant in both continents and therefore illustrates dispersal dynamics, shows that the interchange was initially symmetrical, but followed by an increasing dominance of mammals of North American origin in South America, during the Pleistocene (Marshall *et al.* 1982). Because the fossil record mostly reflects patterns of the temperate regions (Carrillo *et al.* 2015), molecular phylogenies have also been employed to understand the GABI; they show that dispersal from South to North America occurred most likely between the tropical regions of the two continents (Bacon *et al.* 2015). Indeed, many groups of mammals that are found today in tropical forests from Central America originated in the Amazon, and most of the Neotropical placental mammals, such as felids, canids, peccaries, deer, otters, tree squirrels, camelids, as well the extinct proboscideans and horses, are descendants of North Americans migrants (Webb 1991; Antonelli *et al.* 2018).

Global-scale extinction of megafauna impacted the Amazon at the end of the Pleistocene. It reduced megafauna diversity worldwide by two thirds ca. 50,000–10,000 years ago (Barnosky *et al.* 2004). Hunting by humans was an important cause of extinctions, in some regions in synergy with climate change (Barnosky *et al.* 2004; Barnosky and Lindsey, 2010). South America lost ca. 83% of its megafauna during this extinction event, more than any other continent (Barnosky and Lindsey 2010; Prado *et al.* 2015). This loss affected some important ecosystem processes. Because large animals play an important role in the spatial movement of nutrients from areas of high to low nutrient concentration, megafauna extinctions resulted in reduced nutrient flows (Doughty *et al.* 2016a). Extinctions likely reduced the population size of large-seeded tree species that depended on large herbivores for dispersal. In the Amazon basin, the range size of large seeded trees decreased by about 26-31% (Doughty *et al.* 2016b). Furthermore, because fruit size correlates with wood density, the reduction of large-seeded trees dispersed by animals is thought to have reduced the carbon content in the Amazon by ~1.5% after megafauna extinction (Doughty *et al.* 2016b).

The global fossil record shows us that species with specialized diets, larger body sizes, broader geographic distributions, longer life spans, slower reproduction, and fewer offspring, are more susceptible to change and in greater risk of extinction (McKinney 1997; Purvis *et al.* 2000). On the other hand, short-lived species with rapid population growth, more generalist diets, and with high phenotypic plasticity are better suited to adapt and cope with environmental change (Chichorro *et al.* 2019). The Amazonian fossil record of Cenozoic crocodilians and mammals illustrates the same pattern, with large and dietarily-specialized forms occupying large areas that were heavily impacted by environmental change. In the face of environmental pressures currently faced by the Amazon; such as deforestation, hydroelectric dams, and other anthropogenic disturbances; it is possible that species with more specialized diets (Bodmer *et al.* 1997; Benchimol and Peres 2015) might face greater extinction risk (Shahabuddin and Ponte 2005).

Humans may have occupied the Americas much earlier than previously thought, with records dating back to 33,000–31,000 years ago in Mexico (Ardelean *et al.* 2020) and 13,000 years ago in the tropics (Roosevelt *et al.* 2013). As such, human impact on local ecosystems, including the Amazon, has a lengthy history (Levis *et al.* 2017; Watling *et al.* 2017). Studies from multiple disciplines suggest that pre-Columbian human settlements in the Amazon basin were complex and culturally diverse, and that they influenced current patterns of Amazonian biodiversity (Heckenberger and Neves 2009; Shepard and Ramirez 2011).

Although human influence in the Amazon basin has changed through time (see Chapters 8–11), one of the most outstanding legacies of these interactions over many millennia is the abundance and widespread distribution of plant species commonly used by Indigenous peoples. These trees, now identified as “hyperdominant,” include the Brazil nut (*Bertholettia excelsa*), several species of palms (e.g., *Astrocaryum murumuru, Oenocarpus bacaba*), cacao (*Theobroma cacao*), and the caimito (*Pouteria caimito*) (Shepard and Ramirez 2011; Levis *et al.* 2017). These domesticated species have been vital to the livelihood of Amazonian peoples, who have managed the forest for many centuries (Levis *et al.* 2017; Montoya *et al.* 2020).

Accumulating evidence demonstrate that the socially and culturally complex pre-Columbian Amerindians modified the riverine, *terra firme*, and wetland areas of the Amazon, directly impacting the distribution of local species assemblages (Heckenberger 2005; Montoya *et al.* 2020). Examples include anthropogenic soils (*terra preta*) and artificial earthworks such as fish ponds, ring ditches, habitation mounds, and raised fields (Heckenberger and Neves 2009; Prestes-Carneiro *et al.* 2016). The magnitude of these changes varied considerably. In areas such as the Llano de Moxos (Bolivia), natives created a landscape that comprised approximately 4,700 artificial forest islands within a seasonally flooded savannah (Lombardo *et al.* 2020). This region has been confirmed as a hotspot for early plant cultivation, including squash (*Cucurbita* sp.), at about 10,250 calibrated years before present (cal. yr bp), manioc (*Manihot* sp.) at about 10,350 cal. yr bp, and a secondary improvement center for the partially domesticated maize (*Zea mays*), at about 6,850 cal. yr bp (Kistler *et al.* 2018; Lombardo *et al.* 2020).

2.6 Conservation of ecological and evolutionary processes

One key goal of conservation biology is to provide effective principles and tools for preserving biodiversity (Soulé 1985), especially in complex and threatened ecosystems. Critical information for conservation planning in the Amazon is lacking in all major biodiversity dimensions, including taxonomic diversity, geographic distributions, species abundances, phylogenetic relationships, species traits, and species interactions.

The main threats to Amazonian diversity, just like its ecosystems and landscapes, are heterogeneously distributed (RAISG, 2020; Figure 2.9). As such, a one-fits-all strategy will not work in the region. Effective conservation strategies must consider the evolutionary and ecological processes that generate and maintain local species diversity in the many unique biological communities present in this large and ecologically relevant area. However, the legal structure for biodiversity conservation in the Amazon (and globally) is based primarily on individual species. Both governmental initiatives (e.g., Endangered Species Act) and non-governmental policies (e.g., IUCN Red List) are organized around the ideas and actions of species conservation status and threat categories. In a similar manner, measures of deforestation and impacts of infrastructure development, like roads, dams, and waterways, often ignore the compartmentalization of Amazonian diversity, and the unique characteristics of each region and habitat type (Da Silva *et al.* 2005; Latrubesse *et al.* 2017). While current initiatives are crucial, it is important not to lose sight of the processes that keep these species alive and those that generate new diversity.

For instance, when conservation priorities are viewed from an evolutionary standpoint, areas that hold the same number of species may not share the

Figure 2.9 Deforested (red), forested (green), dams (black diamonds), and avian areas of endemism (yellow polygons) in the Amazon. Note the greatest immediate threats to Amazonian biodiversity are located along the agricultural frontier in the southeastern Amazon, especially impacting southeastern areas of endemism. Note the large number of dams in the Andes and on the Brazilian Shield.

same conservation relevance. Instead, the preservation of areas holding distinct, unique, and/or higher amounts of evolutionary lineages should be given higher conservation priority (Forest *et al.* 2007). By prioritizing regions that host widely divergent lineages, higher levels of phylogenetic uniqueness, and a broader spectrum of the genealogy of life (Meffe and Carroll 1994; Figure 2.10), scientists can maximize future options, both for the continuing evolution of life on Earth and for the benefit of society (Forest *et al.* 2007). Maximum levels of global phylogenetic diversity lead to higher ecosystem services globally and higher plant services in general for humankind (Molina-Venegas *et al.* 2021). Conservation priorities based on a deep understanding of how biodiversity patterns have emerged allow us to preserve a potential for future evolution and adaptation (Erwin 1991; Brooks *et al.* 1992). By prioritizing clades that are rapidly speciating and adapting we might, for instance, be able to preserve lineages with higher potential to resist future climatic and ecological change. Likewise, by increasing evolutionary diversity, we are likely to increase trait diversity and to provide increased resilience for Amazon rainforests (Sakschewski *et al.* 2016).

Another way to incorporate evolutionary thinking into conservation is to focus on landscape attributes that generate unique variation or maintain connectivity among populations. Geographic barriers, for instance, restrict species ranges and lead to allopatric diversification (Figure 2.5). In the Amazon, rivers have imposed limits to the distribution of closely related species (Ribas *et al.* 2012). On the other hand, rivers may also be corridors of connectivity for species associated with floodplain habitats.

Free flowing rivers are hence fundamental not only for the species they support, but also for the evolutionary processes that they drive. Similarly, the conservation of regions of steep environmental gradients, which are expected to promote ecological speciation (Figure 2.5), is relevant from an evolutionary standpoint. In the Amazon, for instance, adjacent yet distinct soil types are intimately associated with plant specialization and differentiation (Fine *et al.* 2005). Promoting conservation of these

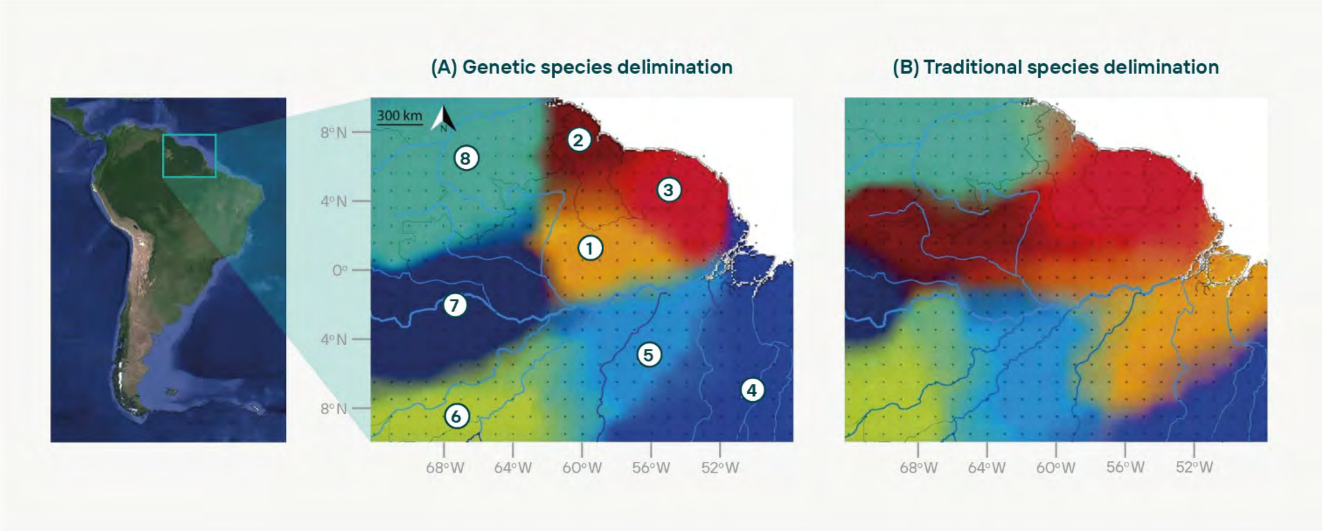


Figure 2.10 Bioregionalization based on species occurrence data for frogs in the eastern Amazon. A. Data from DNA-based species delimitation. B. Data from morphology-based taxonomy. Colors represent affiliations of cells to bioregions. Note both the bioregion boundaries and numbers of endemic species are sensitive to which dataset is used. Images modified from Vacher et al. (2020).

gradients and diverse habitats associated with distinct soil types is therefore important in the short and long term.

The singular diversity of Amazonian organisms was generated over a period of millions of years and represents a large portion of Earth's known and unknown diversity. Because the Amazon has been functioning as a primary source of biodiversity to all other Neotropical biomes (Antonelli *et al.* 2018), forest destruction and species loss have direct impacts on biodiversity and ecosystem function in all other South and Central American regions. Current declines in Amazonian biodiversity (WWF 2016) threaten the evolutionary processes governing the origin and maintenance of species diversity in all of these areas. A strong regional network of biological collections combined with long term monitoring of Amazonian populations, such as those conducted by the RAINFOR network, ForestGeo, PELD, and PPBio programs (PPBio 2005), are urgently needed to improve our understanding of Amazonian biodiversity, ecology, evolution, biogeography, and demography (Stouffer *et al.* 2021).

Apart from taking evolutionary processes into account, conservation efforts in the Amazon must also include the unique ecological aspects of its biota into planning. Organismal habits and behaviors are one important example. The annual migrations of fishes (*piracema*), birds, and insects, as well as tree fruiting blooms, all constitute important biotic resources for human agroecosystems and other natural Amazonian ecosystems. These behaviors are the basis for important ecological phenomena and annual life cycles, including mast flowering, phenological patterns, reproductive booms, and natural flood regimes. Such aspects need to be considered in regional planning and during rainforest conservation efforts. The establishment of river impoundments, for instance, interrupt natural flood regimes and disrupt migration corridors that are critical for the survival of Amazonian freshwater organisms (Winemiller *et al.* 2016; Latrubesse *et al.* 2017; Barthem *et al.* 2017; Albert *et al.* 2020b).

2.7 Conclusions

Amazonian biodiversity, although deeply underestimated, is among the highest on Earth and constitutes the core of the Neotropical realm. This bewildering biodiversity arose from evolutionary diversification over highly heterogeneous landscapes and lengthy time periods in which rates of speciation exceeded those of extinction.

Geological and climatic factors operating over evolutionary time scales (thousands to millions of years) constrained the landscape and riverscape processes that generated heterogeneous soil and water chemistry profiles and other factors, which in turn affected the geographic, demographic, and genetic connections among populations. These abiotic factors strongly affected rates of adaptation, speciation, and extinction, facilitating organismal diversification into major habitat types. Yet, biodiversity itself also contributes to a constant increase in Amazonian species richness, through autocatalytic feedback mechanisms within hyperdiverse Amazonian ecosystems. These biotic interactions lead to the evolution of new traits and to an increase in the structural heterogeneity and functional dimensions of habitats, while enhancing the genetic and phenotypic diversity of Amazonian ecosystems. The interactions of these abiotic and biotic factors allow species to coexist within the same habitats or regions and thereby lower their extinction risks.

Human activities have impacted Amazonian biodiversity for at least 20 Ka. The main effects by Indigenous peoples are observed in plant domestication, agricultural practices, and hunting, all of which altered local vegetation structure and species abundances. Changes to Amazonian ecosystems accelerated in the past 500 years with Portuguese and Spanish colonization, and greatly accelerated again, reaching unsustainable levels, with the transition to modern socio-economic activities during the past 40 years. Rapid changes in land-use for agriculture and other human activities (e.g., logging, mining, hunting, fishing, dams, roads) are profoundly affecting species richness and evolutionary processes by altering the distribution, abundance, connectivity, and ecology of Amazonian species.

Population sizes of many Amazonian species have been falling rapidly in recent years, imperiling many species and degrading the forest biome as a whole (Escobar 2019). The most effective conservation strategies are both dynamic and pluralistic, balancing the irreplaceability, representativeness, and vulnerability of species and ecosystems (Jézéquel *et al.* 2020). Effective conservation planning should maintain population connectivity, dispersal, and gene flow, and ensure the preservation of environmental gradients, all of which facilitate ongoing evolutionary and ecological processes (Anderson *et al.* 2018; Castro *et al.* 2020). Special attention and resources are required in areas of rapid economic and infrastructure development (e.g., road and dam construction), or where major anthropogenic habitat changes have fragmented natural populations via deforestation and degradation for agriculture, cattle ranching, and mining (Benítez-López *et al.* 2019; Stabile *et al.* 2020).

2.8 Recommendations

The global community must work closely and swiftly with national governments whose sovereignty includes Amazonian territory to develop and enact the following scientific and conservation priorities.

Scientific priorities:

- Decade-level financial investments and political support for Amazonian biosciences, prioritizing research and education institutions that enable the study of Amazonian biodiversity at multiple spatial and temporal scales, and training the next generation of Amazonian scientists.
- Biodiversity research and discovery, with support for capacity building, field-based inventories, and surveys to validate and ground-truth remote sensing data. Priorities should be given to universities, research institutions, and collection facilities that enable the long-term archival of biological material, the study of Amazonian ecosystems at multiple geographic, biological, and temporal scales, and training the next generation of integrative Amazonian biologists.
- Integrating “big data” from both the biological and other environmental sciences (e.g., geosciences, climate sciences), combining bioinformatics, genomics, digital morphology from computed tomography (CT) scans, climatic and habitat descriptions, paleoclimatology, tectonics, and other emerging tools, with expert knowledge of species limits, genealogies, current and past environmental descriptions, species interactions, and functional diversity.
- New technologies and capacity building for the genetic and environmental characterization of cryptic and poorly known species, including especially soil and aquatic fungi and microbes.

Conservation Priorities:

- To conserve, preserve, and (where needed) restore terrestrial and aquatic habitat quality and connectivity (habitat corridors).
- To maintain natural processes such as dispersal and gene flow, environmental gradients, and environmental heterogeneity.
- To give specific attention to ecological and evolutionary processes and their conservation, recognizing that they will differ across Amazonian environments and ecosystems.
- To establish and maintain long-term partnerships with local Indigenous and non-Indigenous communities, to exchange critical biodiversity information between academic and local knowledge bases.
- To prioritize conservation action in areas where anthropogenic threats are maximized (e.g., endemicity areas in southeastern Brazil; Figure 2.9).

- To develop ecosystem-level plans for infrastructure, especially water impoundments (e.g., dams) and roads.

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Amazon Assessment Report 2021

Chapter 3

Biological diversity and ecological networks in the Amazon

Dentro da Reserva de Desenvolvimento Sustentável Vitória de Souzel 2018 (Foto: Lilo Clareto/Amazônia Real)

INDEX

Graphical Abstract

- The Amazon basin is one of the most biodiverse areas for most taxonomic groups. However, knowledge of basin-wide richness patterns remains incomplete and its true richness underestimated.
- Diversity varies geographically, with some groups being more diverse in the Amazon lowlands, whereas others thrive in the Andes.
- Plant-animal and trophic interactions are central ecological processes in Amazonian forests, without which these forests would cease to exist.
- Maintaining altitudinal connectivity from the Amazon to the Andes is crucial to conserve Amazon basin biodiversity.

Figure 3.A The Amazon is the most biodiverse area for most taxonomic groups. Photos show iconic species and ecosystems along the altitudinal gradient of the region, as well as selected species interactions. Background illustration by ekolara. Photos by Esteban Suaréz, Galo Zapata-Ríos, Fernando Trujillo, Robert Schlappal/© Superbass / CC-BY-SA-3.0 (via Wikimedia Commons).

Biological Diversity and Ecological Networks in the Amazon

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Key Messages

- The Amazon Basin is one of the most biodiverse areas in the world for most taxonomic groups. Diversity varies geographically, with some groups being more diverse in the Amazonian lowlands, whereas others thrive in the Andes.
- Current evaluations underestimate the true species richness of the Amazon, partially because of the difficulty of sampling in this vast region. The Amazon exhibits an incredibly high rate of discovery of new species (one every second day) and, at the current rate, it will take several hundred years to compile a complete list of plants and animals (not to mention their geographic distribution, natural history, and conservation status). Furthermore, some groups, such as fungi, algae, lichens, and bacteria, are understudied.
- Plant-animal interactions are a central ecological process in Amazonian forests, without which these forests would cease to exist. Such interactions have led to the evolution of high species diversity. These networks of mutualists and consumers determine all aspects of Amazonian forests and are responsible for their composition, species regulation, recovery from disturbance, and the generation of the biodiversity that comprises the forest, rivers, and other ecosystems.

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Abstract

Scientists have not been able to estimate, to the nearest order of magnitude, the number of species in the Amazon. Although the Amazon includes one of the largest forests in the world, it is also one of the least known biologically. Documenting its biodiversity is challenging because of its immense size, heterogeneity, and limited access. Based on current knowledge, the Amazon exhibits the highest density of species as well as the highest number of threatened species (many of them endemic) for vascular and non-vascular plants, fish, amphibians, birds, and mammals. Deeper knowledge of biodiversity patterns is still lacking, and the spatial turnover of species assemblages at different scales remains poorly understood. In the Amazon, we can also find some outstanding examples of animal behavior. For example, many fish migrate over long distances, and some of them perform the longest known freshwater migrations in the world, traveling the entire length of the Amazon Basin in a round trip migration of~12,000 km. It is also important to consider that plant-animal interactions and trophic interactions are central ecological processes in Amazonian forests. Disruptions of these interactions can alter forest community composition over the long-term. Functional diversity, including intra- and inter-specific variation, has recently attracted the attention of scientists, and it is evident that it contributes to community and ecosystem resilience to perturbations, including climate change. There is still much to learn about Amazonian biodiversity, species assemblages, and ecological interactions. There are spatial and taxonomic biases in the data (including many unexplored locations and lesser-known taxonomic groups), which affect our understanding of biodiversity patterns in the Amazon. This chapter highlights the need for more basic and applied research to improve our knowledge of biodiversity patterns across the region. This information is critical for understanding the impacts of human activities and informing conservation and restoration actions.

Keywords: Biodiversity, species richness, endemism, fauna, flora, fauna, plant-animal interactions, migration, phylogenetic diversity, functional diversity.

3.1 Why is the Amazon so rich in species and ecosystems?

The Amazon is the most biologically diverse area on the planet. Encompassing approximately 5,800,000 km^2, the biodiversity in the Amazon biogeographic province is incommensurable. More than one tenth of the world's species occur in this region (Mittermeier *et al.* 2002). Assessments of species richness indicate close to 50,000 vascular plants, at least 2,406 fishes in the Amazon Basin, and 427 amphibians, 371 reptiles, 1,300 birds, and 425 mammals in the Amazon rainforest (Mittermeier et al, 2003, Hubell *et al.* 2008, Jézéquel *et al.* 2020). These numbers are gross underestimations of the real numbers, and for some groups are biased to the Brazilian Amazon (http://censo.museugoeldi.br:8080/museugoeldi-web-1.2.0). In addition, these numbers highlight the need for more basic research on biodiversity patterns throughout the region (see Box 3.2 for estimates of species richness numbers that include the Andean section of the Basin, based on records from the Global Biodiversity Information Facility, GBIF). Endemism is also high in the Amazon Basin. For example, in the Amazonian lowlands approximately 40% of mammals, 70% of reptiles, and 86% of amphibians are not found elsewhere (Mittermeier *et al.* 2003). Amazonian ecosystems range from forests and savannas to wetlands (see Chapter 4). The three main types of water (white-, black-, and clear-waters) differ in their origin and composition of sediments and minerals, forming a unique mosaic of freshwater ecosystems throughout the Basin (see Chapter 4). The diversity of life in the Amazon is astonishing, but why is the Amazon so rich in species and ecosystems? Many processes have contributed to generate the high Amazonian biodiversity (see Chapter 2 for different models of diversification). Variables including tectonics, hydroclimate, evolutionary and ecological factors (see Chapter 2), disturbance regimes, and the more recent legacy of a cultural landscape (see Chapter 10) are among the most important processes.

Biodiversity refers to the number of species, the variety, and variability of living organisms (*e.g.*, plants, animals, fungi, microorganisms), including terrestrial, subterranean, marine, and other aquatic ecosystems, and the ecological complexes of which they are a part. Included in the concept of biodiversity is the variety within species (genetic diversity), between species, and of ecosystems (UN Convention on Biological Diversity, https://www.cbd.int/convention/articles/?a =cbd-02). Scientists have not yet estimated to the nearest order of magnitude the number of species living in the Amazon. Researchers continue to discover new species, even among the best-known taxonomic groups, such as mammals and birds (Patterson 2001, Milá *et al.* 2012, Ribas and Aleixo 2019). For many invertebrate taxa, undescribed biodiversity is so prevalent that scientists have described only a small fraction of the species that occur in the region.

The Amazon is a global icon of biodiversity. Current knowledge on the distribution of species suggests complex biogeographic patterns (Ribas *et al.* 2012, Naka and Brumfield 2018, Silva *et al.* 2019, Moraes *et al.* 2020). After considering these biogeographic patterns and the geological and climatic history of the region, researchers have proposed several hypotheses to explain the origin of high Amazonian biodiversity (Haffer 2008, Leite and Rogers 2013). The relationship between biological, climate, and geological data (Baker *et al.* 2014) is important to elucidate the environmental history, origin, and fate of Amazonian biodiversity. However, biogeographic patterns vary considerably among taxonomic grou-ps, adding complexity to the analysis of environmental history and biotic diversification.

The establishment of a transcontinental drainage system during the Miocene (9.4 to 9.0 Ma) may have promoted the recent evolution of *terra firme* communities in the lowlands of the western Amazon (Hoorn *et al.* 2010, Ribas and Aleixo 2019). In contrast, the different flooded habitats depend on the environments associated with river dynamics and the cycle of floods (the flood pulse), so their evolution is linked to the broad Amazon drainage system (Toews *et al.* 2016, Moraes *et al.* 2016). Riverine dynamics could have influenced the recent evolution and distribution of species adapted to flooded environments and possibly interrupted movement between eastern and western populations of the Amazon, as suggested by phenotypic variation in vertebrates and confirmed by genomic analyses (e.g., Leite and Rogers 2013). In addition, as a response to broader geological changes, most species were able to generate different degrees of intraspecific genetic diversity, depending on how they responded to physical changes in their habitats (Ribas and Aleixo 2019). Therefore, another fundamental driver for regional biological diversity is the environmental heterogeneity associated with the rise of the Andes, and the pulse and fluctuation of seasonal floods in the great alluvial river plains of the Amazon, complemented by macro-regional climatic events (Junk 1997).

This chapter provides an overview of biodiversity in the Amazon region, explains why this region is so rich in species and ecosystems, and outlines some outstanding ecological processes that make the Amazon an icon of the natural world. Selected terrestrial and aquatic taxonomic grou-ps exhibit how much we know and more importantly how much we still do not know and have to discover. A clear understanding of biodiversity levels and their spatial and temporal variations is crucial to understanding future stability under different climate-change scenarios, and informing conservation efforts.

3.2 Biological diversity patterns of selected taxonomic groups

3.2.1 Vascular Plants

Intangible oral transmission perpetuated traditional knowledge, agricultural practices, medicinal uses, and culinary uses of Amazonian plants from generation to generation. Pictorial depictions in artifacts (e.g., textiles, pottery, jewelry) and archeological remnants left across the land (see for example Mesía Montenegro 2014, Zarillo *et al.* 2018) point to traditional uses and domestication of many plants (Box 3.1). The first Europe-ans chronicled and illustrated domesticated plants, such as chili pepper, cassava, and tobacco, as well as the first illustration and delicious description of the pineapple (Cobo 1964[1653], Fernández de Oviedo and Valdés 1526, Myers 2007, Piso and Marcgrave

1648). Despite the long traditional use of some of these plants, the potential benefits of the vast majority of species are still unknown (Alcantara-Rodriguez 2019, Antonelli *et al.* 2019, National Research Council 1989). The Spanish crown financed botanical expeditions to the South American colonies in the eighteenth century with the goal of discovering and documenting medicinal plants, such as quinine (cascarilla bark, *Cinchona officinalis*; Ruiz 1792, Ruiz and Pavón 1801). These early expeditions, along with later European ones, collected thousands of herbarium specimens and published works that built the foundation of modern Amazonian plant taxonomy (e.g., Aublet 1775, French Guiana; Ruiz and Pavón 1798–1802, Peru; Humboldt and Bonpland 1816–1818, northern South America; von Martius and collaborators 1840–1906, Brazil, at the time the first complete flora of a South American country). In the nineteenth century, the first museums and associated herbaria opened in the nascent republics (National Museum in Rio de Janeiro in 1831, Quito Central University in 1860, Museu Paraénse Emílio Goeldi in 1866, Georgetown University in 1879, Rio de Janeiro Botanical Garden in 1890), followed by many others at the turn of the twentieth century. During the second half of the twentieth century, numerous in-country initiatives and international collaborations in botanical research and exploration resulted in new herbaria in museums and universities, thousands of specimens collected, new species of plants described for science, and an array of floristic research publications. In the last thirty years, with the advancement of electronic resources (virtual herbaria, digital libraries, databases) plant catalogues or checklists (a curated list of species names) became a faster way to compile information and have been published for each country (BFG 2018, Ulloa Ulloa *et al.* 2017, Ulloa Ulloa and Jørgensen 2018, Table 3.1). There is still no complete modern flora (in the form of revisionary descriptive work, with identifications keys, and illustrations) for any country in the region, but innovative online collaborations are underway (Table 3.1). A recent compilation of a list of vascular plants of the Americas (Ulloa Ulloa *et al.* 2017) synthesized the remarkable achievements of plant expeditions, collectors, and describers, regional floras, and tens of thousands of publications (Givnish, 2017). The Amazonian countries (Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, Guyana, Suriname, and the French overseas department of French Guiana) are known to harbor some 79,600 species of native vascular plants, which correspond to 20% of all of the world's plants (Ulloa Ulloa *et al.* 2017, 2020; Nic Lughadha *et al.* 2016; Table 3.1). Approximately 4% of the plant species descriptions were added from 2017 to 2020, and of the 79,600 vascular plants currently known, 61% (48,531) are endemic (Ulloa Ulloa *et al.* 2020, Table 3.1, Figure 3.1). There is no authoritative list of all of vascular plants of the Amazon Basin, but estimates for seed plants occurring below 1,000 m vary from 14,000 to 50,000 species (Gentry *et al.* 1997, Lewinsohn and Prado 2005, Cardoso *et al.* 2017). Estimates for lowland trees varies between 6,000 and 16,000 species, including at least 1,000 flood-resistant trees and 388 herbaceous plants (Junk and Piedade 1993; Cardoso *et al.* 2017; ter Steege *et al.* 2016, 2020), emphasizing our imperfect knowledge of the richness for Amazonian plants.

Human activities may threaten many Amazonian plant species, particularly those with restricted geographical ranges (Ulloa Ulloa *et al.* 2017). The IUCN (International Union for Conservation of Nature, 2001) Red List categories were used to assess the conservation status of endemic plants of Ecuador (León-Yánez *et al.* 2011), Peru (León *et al.* 2006), and Brazil (Martins *et al.* 2018). Sixty-five percent of the endemic species evaluated (8,564) are threatened, i.e., listed as Critically Endangered (CR), Endangered (EN), or Vulnerable (VU) in the IUCN Red List of Threatened Species (Figure 3.2). This percentage is well above the world wide estimated risk for tropical countries of 47% (Pitman and Jørgensen 2002). In addition, 2,011 endemic species were Data Deficient (i.e., without enough information for a detailed assessment), which could underestimate the number of threatened species. Poorly known species could become extinct without even being reported (Humphreys *et al.* 2019). The endemic plants evaluated from Ecuador, Peru, and Brazil (13,165 species) combined represent approximately 19% of all endemic species (*ca.* 67,900) from tropical South America (Ulloa Ulloa *et al.* 2017, Figure 3.2). For Ecuador alone, 78% of endemic plant species are under risk due to deforestation or habitat alteration (León-Yánez *et*

Table 3.1. Native vascular plant (all plants) diversity in Amazonian countries and references.

Country/Region	Guianas (Guyana, Suriname, French Guiana)	Venezuela	Colombia	Ecuador	Peru	Bolivia	Brazil
Total Vascular Plants (Numbers in parenthesis are total number of endemic species) **(Ulloa Ulloa *et al.* 2020)**	**8,389** (1,183)	**15,395** (3,475)	**24,047** (7,420)	**18,505** (5,992)	**19,836** (7,875)	**14,736** (3,097)	**34,472** (19,489)
Below 1000 m, Seed Plants (Cardoso *et al.* 2017 or specified)	**6,890** [incl. Venezuela]		**5,835** (Bernal *et al.* 2015)	**3,607**	**5,401**	**3,518**	**11,846** (BFG 2018)
Ongoing Country Flora	**Flora of the Guianas** (Görts-van Rijn and collaborators 1986–present)	**Flora de Venezuela** (Lasser *et al.* editors (1968–present) **Flora of the Venezuelan Guayana** (Steyermark *et al.* 1995–2005)	**Flora de Colombia** (1983–present)	**Flora of Ecuador** (Sparre *et al.* editors, 1973–present).	**Flora of Peru** (MacBride and collaborators 1936–present, see Gentry, 1980)	**Flora de Bolivia** (In preparation, see Menezes *et al.* 2015)	**Flora do Brasil 2020** online
Catalogue of Plants	**Funk *et al.* (2007); Feuillet (2009)**	**Hokche et *al.* (2008).**	**Bernal *et al.* (2015)**	**Jørgensen and León-Yánez (1999); Ulloa Ulloa and Neill (2005); Neill and Ulloa Ulloa (2011)**	**Brako and Zarucchi (1993); Ulloa Ulloa *et al.* (2004)**	**Jørgensen *et al.* (2014)**	**Forzza *et al.* (2010); BFG (2018)**
Red List Endemics		**Huérfano *et al.* (2020)**	Ongoing (**Calderón *et al.* 2002–present**, not exclusive to endemic plants)	**León-Yánez *et al.* 2011**	**León *et al.* (2006 [2007])**	Ongoing (**Navarro *et al.* 2012–present**)	**Martins *et al.* (2018)**
Useful / Medicinal Plants. There are numerous local and regional publications. Only country wide are cited here.		**Guánchez (1999)**	**Pérez Arbelaez (1956, 1990)**	**De La Torre *et al.* (2008); Ríos *et al.* (2007)**	**Brack Egg (1999), Reynel (2003).**		See **Dutra *et al.* (2016); Vieira *et al.* (2016); Coradin *et al.* (2018) Mors *et al.*, (2000), Modolo and Foglio (2019)**
Regional	**Correa Q. (1989); National Research Council (1989); Estrella (1995), Villachica (1996), Tejedor Garavito *et al.* (2012)**						

Figure 3.1 Number of vascular plants in Amazonian countries. For each area, the total number of species of native vascular plants and the number of endemic species (in parenthesis) are indicated (Data from Ulloa Ulloa *et al.* 2020. Illustration by C. Ulloa Ulloa).

al. 2011). Although national Red Lists and Red Data Books may be restricted geographically, they provide an overview of their status and a basis for conservation actions (Pitman and Jørgensen 2002).

3.2.2 Fungi, algae, and non-vascular plants

Non-vascular plants (liverworts, hornworts, mosses), algae, and fungi are the main drivers of the carbon and nutrient cycle at high altitude (Beringer *et al.* 2001, Lang *et al.* 2009). Biogeographically, the difference in the abundance of non-vascular plants in the Amazon is lower compared with Andean forests. As with vascular plants, non-vascular plants have their center of diversity in the tropical Andes, although there species diversity increase with altitude. Often overlooked in these habitats, the total diversity of these taxa is typically underestimated (Ferris *et al.* 1996).

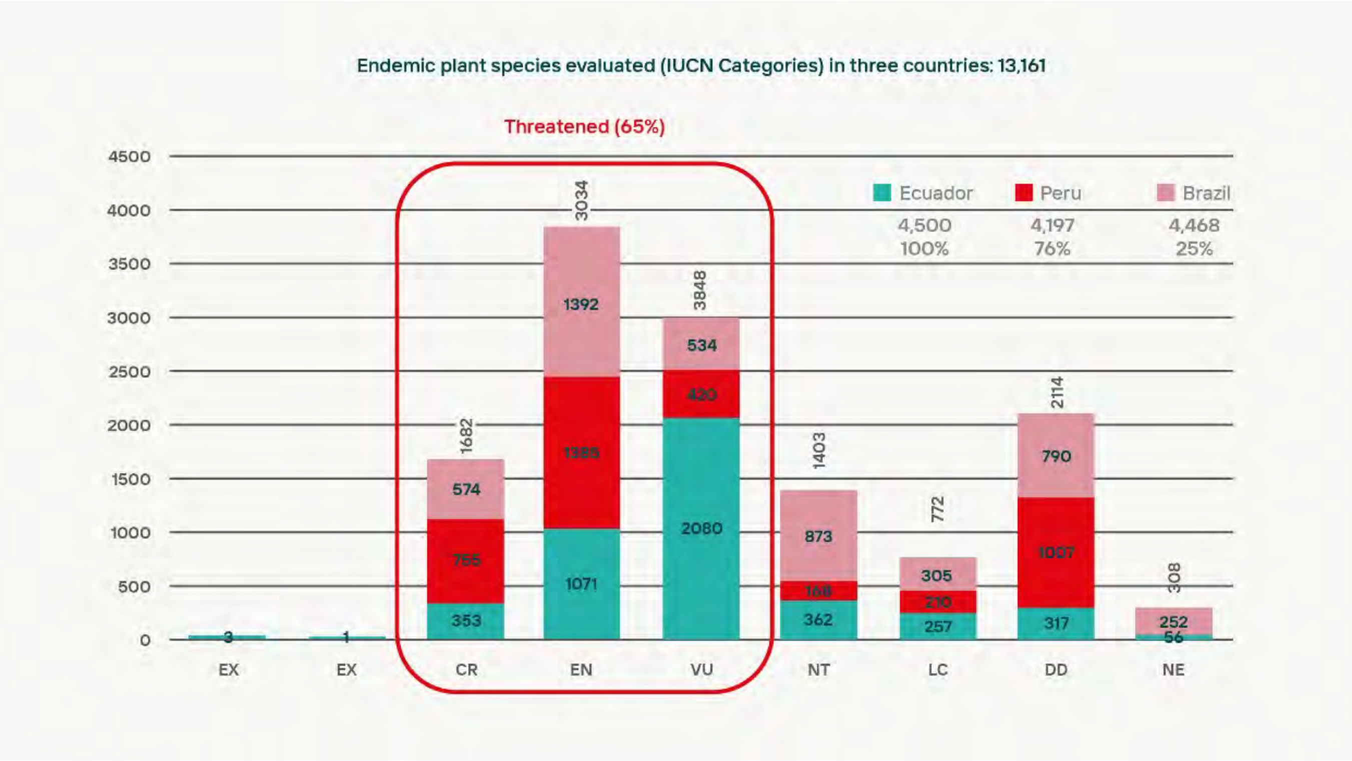


Figure 3.2 Plant endemics (all plants) of Brazil, Peru, and Ecuador evaluated with IUCN conservation status categories. The red rectangle encloses the three threatened IUCN Red List categories. IUCN categories: EX=Extinct; EW=Extinct in the Wild; CR=Critically Endangered; EN=Endangered; VU=Vulnerable; NT=Not Threatened; LC=Least Concern; DD=Data Deficient; NE=Not Evaluated. Number of endemic plant species evaluated: Ecuador 4,500 (100% of endemics, León-Yánez *et al.* 2011), Peru 4,197 (76%, León *et al.* 2007), Brazil 4,468 (25%, Martins *et al.* 2018).

There are a large number of species of algae and, although the bibliographic references significantly differ in the estimates of the number of species, it is believed that there are between 30,000 and 50,000 species, of which only half have been described (Dos Santos 2016). The information available on algae for the Amazon is very scarce; no research has attempted to characterize the flora of microalgae or subaerial algae of these forests and examine their biodiversity in detail using state-of-the-art methods (Lopez-Bautista *et al.* 2007). Presenting a synthesis of the biodiversity status of tropical forest algae is difficult or even impossible (Andersen, 1992).

Fungi, on the other hand, belong to their own kingdom, and are different organisms from plants and animals because they excrete digestive enzymes and absorb externally digested nutrients. Although the factors that determine their diversity remain little explored, estimates of the number of species on the planet vary from 500,000 to almost 10 million. Recent studies have suggested that fungal diversity is greater in the lowlands than in Andean slopes (Arnold and Lutzoni 2007; Tedersoo *et al.* 2014), but the later have been considerably less studied (Barnes *et al.* 2016). Lichens are composed of two organisms living symbiotically: fungi and photosynthetic algal cells. These organisms are one of the most diverse components of the Amazon forest (Sipman and Aptroot 2001, Lucking *et al.* 2009). The corticolous and foliicolous groups are much more diverse than the saxicolous species (Lucking 2008). The excessive amount of litter in these forests limits the diversity of terrestrial lichens; however, there are some records of them on the banks or landslides on the sides of roads.

Finally, mosses represent the dominant vegetation cover in a wide range of ecosystems, especially those that thrive in cold stress environments, where they typically adopt a cushion shape. However, the diversity of mosses in the Amazon is relatively low. Although 40 to 50 species can be found in any particular site, the increase in additional species from one site to another is low (Gradstein *et al.* 2001). In general, knowledge about the diversity of cryptogams is very limited (Scott *et al.* 1987, Brehm *et al.* 2008). Therefore, a comparison of the Amazon with the tropical Andes and surrounding areas can only be based on estimates using the high turnover in species composition along elevation gradients. The diversity of this group of plants could be related to climatic, edaphic, and floristic factors, but it is constant humidity that favors the growth of this group of plants (Chaverri-Polini 1998).

3.2.3 Diversity of insects

Although insects dominate terrestrial ecosystems (by the number of species or total biomass), the richness of insects in the region is completely unknown (Adis 2007, Hanson and Nishida 2016). Amazonian entomofauna is amazingly rich all along vertical forest strata, and it would be expected that the patterns of distribution of species at large spatial scales are not even across the region (Lucky *et al.* 2002, Erwin *et al.* 2005). High numbers of species coupled with high population densities are attributed to Amazonian insects, especially those inhabiting the forest canopy (e.g., Adis *et al.* 1998, Erwin 1998). For example, Formicidae (the ants) and Diptera (flies, mosquitoes, and their kin) represented 52% and 10%, respectively, of the more than 300 arthropods per square meter obtained by fogging the canopy.

In addition, a total of 95 different ant species were found on a single tree, as many as the entire indigenous ant fauna of Germany (Adis 2007). Very limited information is available about the centers of evolution and dispersal of insects, and other arthropods, that occur in the Amazon. Available data (*e.g.*, Erwin 1998, Adis 2007) suggests that some groups originated in the neotropics and are widely distributed beyond the borders of the Amazon (*e.g.*, leafcutter ants, *Atta* spp.); while other groups originated along the Andes or the Guyana shield, with a subsequent dispersal into the Amazon Basin (*e.g.*, Meinertellidae); and still others originated in the Amazon, along the floodplains of major tributaries (*e.g.*, some Carabidae).

Currently, it is difficult to predict whether changes in community composition are related to differences in vegetation types, soil, climate, human disturbance, or a very subtle combination of all of these factors. Probably, a different suite of factors affects different taxa and accounts for the observed patterns (*e.g.*, Erwin *et al.* 2005, Oliveira *et al.* 2010, Solar *et al.* 2016). In contrast to the amount of information available for terrestrial insects and arthropods, aquatic arthropod communities are much better known as a result of monitoring of water quality (*e.g.*, Heckman 2011, Hamada *et al.* 2014).

Many studies of Amazonian aquatic insects have examined water quality because of the insects' sensitivity to forest loss and other anthropic changes (Hamada *et al.* 2014), particularly the larval forms of groups such as Ephemeroptera, Trichoptera, Diptera, Plecoptera, and Odonata (Brito *et al.* 2020). Deforestation-induced reduction of aquatic insects can also affect the ichthyofauna, because aquatic larvae of many insects are the principal source of food for many small and medium species of fishes. One of the biggest challenges is to systematize the taxonomic kno-wledge of aquatic insects and other macroinvertebrates (Hamada *et al.* 2014) in the different aquatic ecosystems of the Amazon.

The high diversity of aquatic fauna is associated with the environmental heterogeneity of aquatic Amazonian ecosystems. Species from ten insect orders are specialized aquatic or semi-aquatic habits. The order Diptera stands out, which holds half of the known aquatic insects, notably Chironomidae (Trivinho-Strixino 2019). Several taxa are considered aquatic bioindicators because of their dependence on the aquatic environment for at least some stage of their life. The maintenance of riparian forests prevents the loss of species and ecosystem services provided by aquatic insect communities (Dala'Corte *et al.* 2020, Dias-Silva *et al.* 2020). When updating the list of Trichoptera, Paprocki and França (2014) found an increase of more than 65% in the number of species, of which 90%

Box 3.1 Domestication of plants and human influence

The Amazon Basin has a long history of human occupation, and cultivation and domestication of numerous plants (Young *et al.* 2007, Pearsall 2008, Piperno 2011, Clement *et al.* 2016) (Figure B3.1.1). At the time of European contact, over one hundred native plant species were already cultivated both in the high Andes and lowland Amazon, including beans, cacao, manioc, chili peppers, peanuts, potato, sweet potato, numerous fruit trees, palms, and many other tropical American species introduced to the region (Pearsall 2008; Piperno 2011; Clement et al. 2010, 2015; Levis et al. 2017; Lombardo et al. 2020). However, the imposition of colonial European agricultural methods and crops from the eastern hemisphere relegated most of those native species to local consumption and only a handful became of worldwide importance (National Research Council 1989, Ulloa Ulloa 2006, Young et al. 2007). However, a few species still have high importance in the region (Alexiades and Shanley 2004, Shanley et al. 2011 FAO).

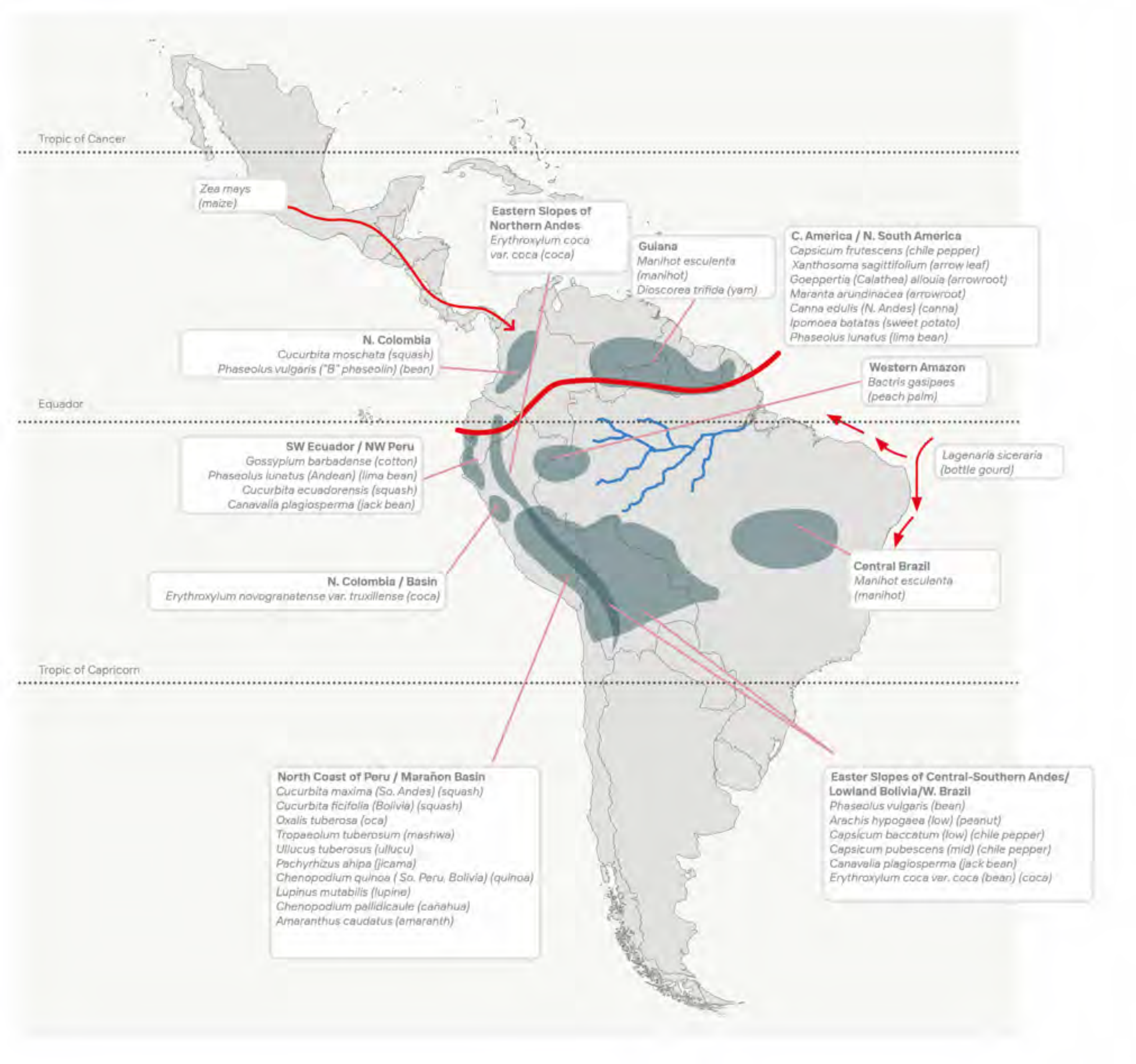


Figure B3.1.1 Areas of origin of domesticated plants (adapted from Pearsall, 2008).

The Andes region provided the world with the potato (*Solanum tuberosum* complex), tomato (*Solanum esculentum*), bell pepper and *ajíes* (*Capsicum* spp.), and beans (*Physallis* species), selected and genetically-manipulated beginning thousands of years ago (Raimondi and Camadro 2003, Rodríguez-Burrouzo *et al*. 2003, Pearsall 2008).

Lesser-known tuber species include *Arracacia xanthorrihiza* (aracacha, zanahoria blanca), *Oxalis tuberosa* (oca), *Tropaeolum tuberosum* (mashua), and *Ullucus tuberosus* (melloco or ulluco) (National Research Council 1989). Among the pseudocereals, *Chenopodium quinoa* (quinua) has recently arrived in international markets and has become an important food in gluten-free diets. Fruit trees originating from the Andes are the tree tomato (*Solanum betaceaum*), papaya (*Carica* papaya), lucuma (*Pouteria lucuma*), various species of the legume genus *Inga*, and shrubs such as naranjilla (*Solanum quitoense*), sweet cucumber (*Solanum muricatum*), goldenberry or uvillla (*Physalis peruviana*), and no fewer than ten species of passion fruits (maracuyá, species of *Passiflora*). Some of these plants have made their way into international markets through cultivation in New Zealand and California (Young *et al.* 2007).

Among multipurpose plant species that have been derived from human propagation and selection are the palms (Arecaceae). Palm species in the Amazon were first reported by Wallace (1853) as being useful to local inhabitants, and this was the first of a series of regional efforts on ethnobotanical research, at the local and regional levels, and assessments of domestication examples (Clement et al. 2010). When palm harvest takes place on communal properties, peasants overexploit their resources (Balslev et al. 2015). The majority of native palms from the tropical Andes (Colombia to Bolivia, 67% of the 336 species) have different uses and applications including food, construction, and oil (Valencia et al. 2013, Moraes et al. 2015). While exploring Venezuela, Humboldt and Bonpland (1805) collected and described to science the Brazil nut, *Berthollettia excelsa* (Lecythidaceae), a species of tree already well known long before the arrival of European explorers, and widely spread across the lowland Amazon. Recent analyses of tree species composition of lowland Amazonian forests revealed "hyperdominance" of a few species, particularly domesticated species such as the Brazil nut and various palm species, indicating that modern tree communities in the lowland Amazon may be structured, to an important extent, by a long history of plant domestication by Amazonian peoples (ter Steege et al. 2013, Levis et al. 2017). Forest patches dominated by one or a few useful plants are possibly the result of management practices over millenia (such as controlled burning, seed planting, or soil improvement) that have altered plant species composition (Levis et al. 2018, Silva et al. 2021). Other case studies show that the Amazon offers an impressive list of categories of useful plants that have also been part of domestication processes. *Bixa orellana*, achiote or annatto, long used in tropical America and worldwide in the cosmetic industry and as food coloring, was probably domesticated in northern South America (Moreira et al. 2015). Recent research revealed traces of cacao (*Theobroma cacao*) in an archeological site in the foothills of the Ecuadorian Andes dating back 5,300 years (Zarillo et al. 2018). The use of *Anadenanthera colubrina* (vilca, curupay, Fabaceae) powder — a psychoactive South American plant with a wide distribution — may have been particularly important for the Tiwanacota culture (600–1,000 A.D.) in Bolivia near Lake Titicaca (Pochettino et al. 1999); its use was then widely disseminated, coinciding with seasonal dry forests between 300—2,200 m (Kvist and Moraes 2006). The Amazon basin is a center of diversity for cotton, such as the most widely distributed *Gossypium barbadense* (Malvaceae), which is the second most cultivated species, and known for the best fiber quality (Liu *et al.*2015). Important crops likely originating in the southwestern Amazon are manioc (*Manihot esculenta*), peach palm (*Bactris gasipaes*), and peanuts (*Arachis hypogea*) (Clement et al., 2016). The most important medicine from the Andes is quinine (cascarilla, quinina), irrationally exploited and used for centuries to control malaria (Crawford 2016; Ortiz Crespo 1995, 2002; Ulloa Ulloa 2006 [2007]). Originally extracted from the bark of the cloud forest tree genus *Cinchona*, the alkaloid is nowadays synthetically produced and found in the bitter flavor of tonic water (Ulloa Ulloa 2016 [2007). The coca plant (*Erythroxylum coca*) grows on warm Andean slopes, and the leaves have been socially chewed or drunk as tea (mate de coca) for centuries, especially in Peru and Bolivia, as a stimulant, and to help with the effects of high-altitude sickness.

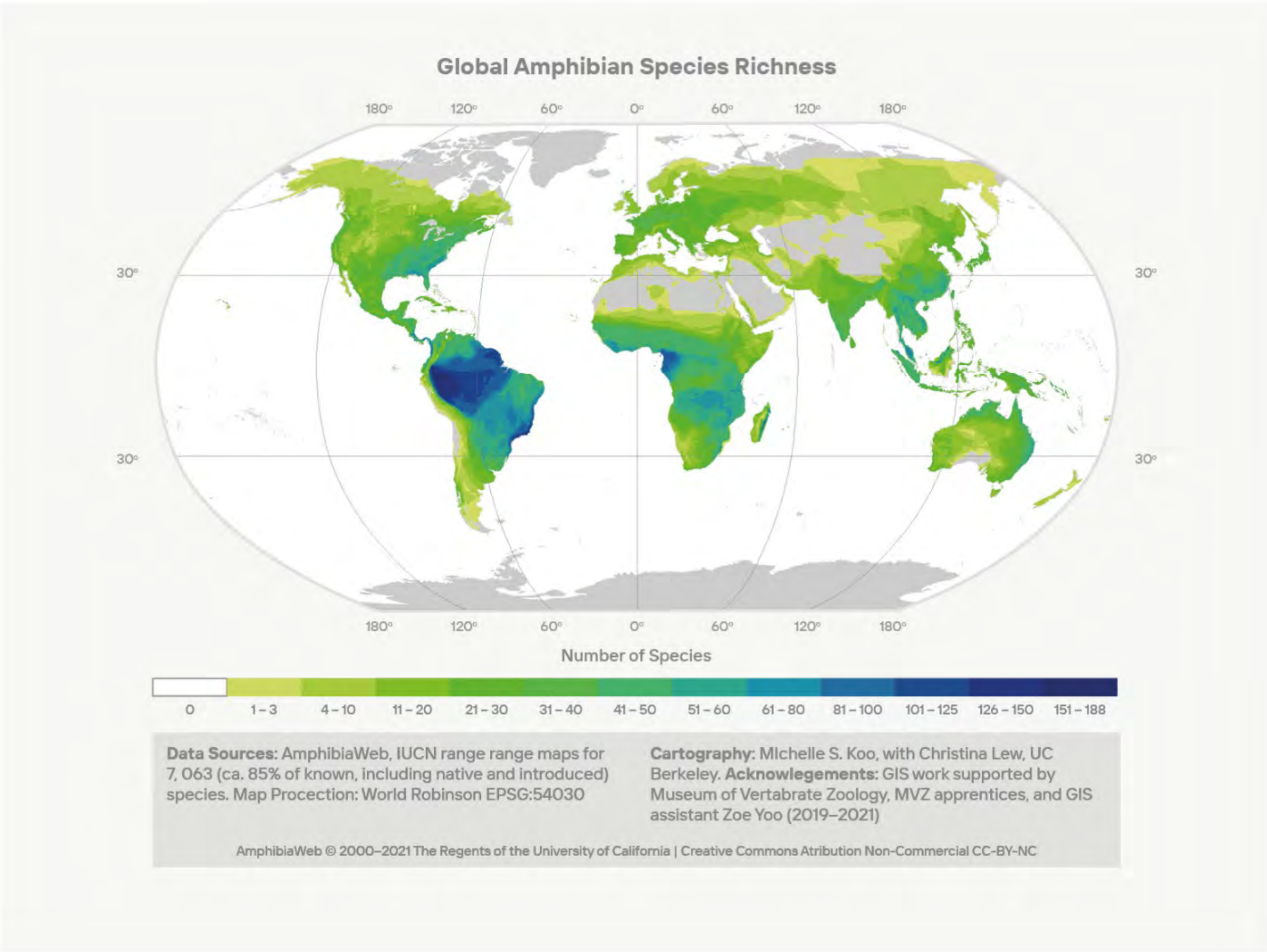
were new species to science, in addition to new records for Brazil. Elmidae, one of the four largest aquatic Coleoptera families, had the first checklist of Amazonian Elmidae species published in the last decade by Passos *et al.* (2010). There is an increasing number of new records and descriptions of genera and species for the Amazon region (*e.g.*, Menezes *et al.* 2018, Almeida *et al.* 2020). However, much is still unknown. The formation of taxonomists, strengthening of collections, and a continuous increase in the rate of description of new species can reduce this knowledge gap (Rafael *et al.* 2009).

3.2.4 Diversity of fish

The Amazon basin contains the world's most diverse freshwater-strict fish fauna, with 2,406 valid species belonging to 514 genera, 56 families, and 18 orders (Jézéquel *et al.* 2020). This exceptional diversity, which represents approximately 15% of the world's freshwater fishes, includes 58% of species found nowhere else on earth (1,402 endemics, Jézéquel *et al.* 2020). Part of this diversity also includes marine taxa that have adapted to freshwater, such as the diverse Amazon stingrays. Unlike many other river basins of the world, where species richness increases downstream along fluvial gradients (Muneepeerakul *et al.* 2008, Ibañez *et al.* 2009), species diversity and endemism show decreasing west–east gradients in the Amazon Basin, suggesting that contemporary Amazonian fish fauna originated in and colonized from the western portion of the Basin (Oberdorff *et al.* 2019). This pattern of fish diversity also indicates that the colonization of the eastern portion of the Basin is still incomplete and is interpreted by the authors as consistent with the recent establishment of the modern Amazon River in roughly the last 2.5 Ma, a topic still largely debated.

The importance of species richness to ecosystem stability, function, and resilience depends on the diversity and values of the species' traits (functional diversity), and on the degree of functional redundancy (degree of similarity in the functional characteristics) among species assemblages (Flynn *et al.* 2009, Mouillot *et al.* 2013, Kelley *et al.* 2018). The Amazon Basin not only has the world highest freshwater fish diversity, but also the highest functional diversity (Toussaint *et al.* 2016). Although functional diversity usually increases with taxonomic diversity, the functional diversity of Amazonian fish fauna is much larger than expected from its already exceptional diversity (Toussaint *et al.* 2016), probably reflecting the extremely rich variability of local environmental conditions (Leitaõ *et al.* 2018, Benone *et al.* 2020).

Fish species diversity in the Amazon Basin includes a large array of forms (including dorso-ventrally or laterally flattened, anguilliform, or globe-shaped species), colors, adaptations (*e.g.*, to the low oxygen concentrations found in floodplains), trophic habits (blood sucking, scale eating, or the arahuana [*Osteoglossum bicirrhosum*] jumping several meters out of the water to feed on insects, spiders, birds, or reptiles on tree branches), and reproductive adaptations (*e.g., Copeina arnoldi* that spawn on terrestrial plant leaves, reviewed in Carvalho *et al.* 2007). It also includes a wide variety of sizes, from miniature species that either mature under 20 mm of standard body length or do not exceed a maximum of 26 mm (Weitzman and Vari 1988), to large species that reach 3 m or more in length, like the pirarucu (paiche, *Arapaima gigas*) or the goliath catfish *Brachyplatystoma filamentosum*, both weighing more than 200 kg (Nelson 1994, Lundberg and Littmann 2003). Many of the small and miniature species are exploited as aquarium fish and sustain an important international ornamental trade, where the main export markets are Asia, Europe, and North America (Andrews 1990, Anjos *et al.* 2009, Evers *et al.* 2019). This trade also includes some large species that are caught and exported in juvenile stages, such as many pimelodid catfishes (*Brachyplatystoma* spp., *Pseudoplatystoma* spp., etc.), or the Amazonian arowanas (Moreau and Coomes 2006). In contrast, medium-sized and large species (mostly belonging to the Order Characiform and Siluriform, but also Perciform, Cichliform, Clupeiform, or Osteoglossiform) support important fisheries throughout the Basin and serve as an economic sopportunity and main source of animal protein for many of the inhabitants of the Amazon Basin (Barthem and Goulding 2007, Duponchelle *et al.* 2021).



Data Sources: AmphibiaWeb, IUCN range range maps for 7, 063 (ca. 85% of known, including native and introduced) species. Map Procection: World Robinson EPSG:54030

Cartography: MIchelle S. Koo, with Christina Lew, UC Berkeley. **Acknowlegements:** GIS work supported by Museum of Vertabrate Zoology, MVZ apprentices, and GIS assistant Zoe Yoo (2019–2021)

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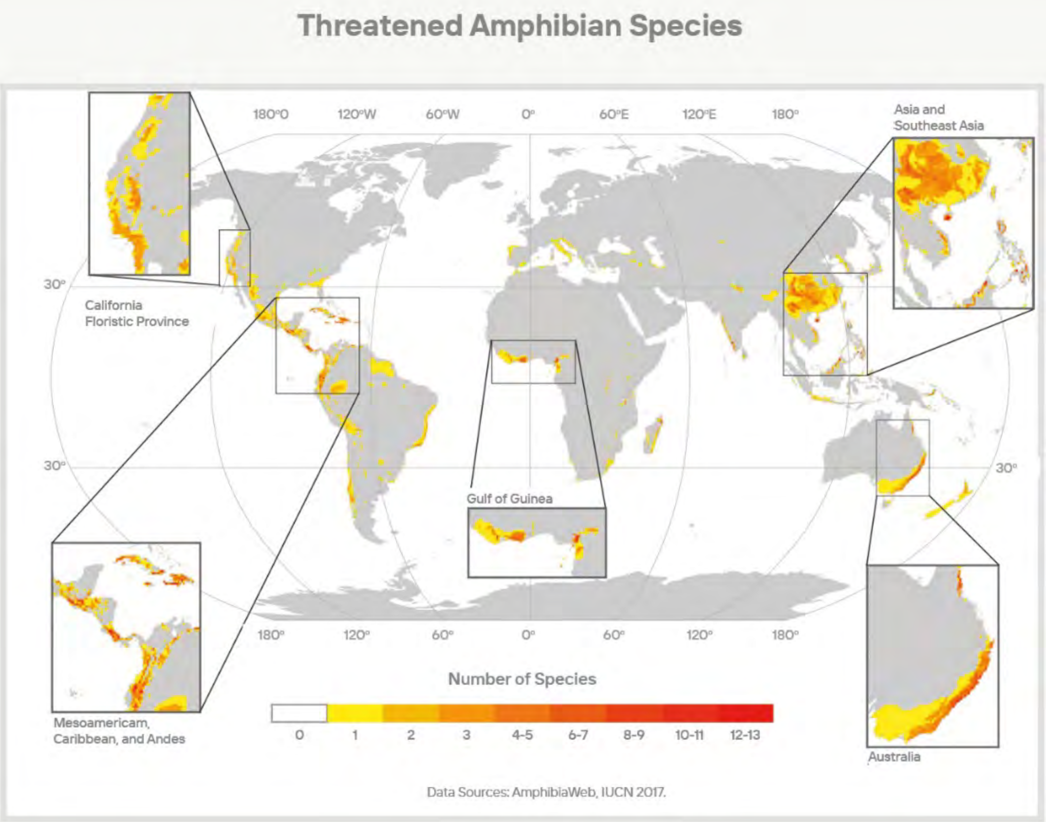
Figure 3.3 Global species richness of amphibians. Note the high alpha diversity in the lowland Amazonian rainforest. Source: AmphibiaWeb (2020).

3.2.5 Diversity of Amphibians

Amphibians are an ecologically and behaviorally diverse group of vertebrates containing 8,380 species (Frost 2021) that range from the familiar (frogs, toads, and salamanders), to the fossorial caecilians (Duellman and Trueb 1986, Wells 2013) (Figure 3.3). The Amazon Basin exhibits the highest density of species in the world, and one of the highest number of endangered species (AmphibiaWeb 2020, Bass *et al.* 2010, Scheele *et al.* 2019) (Figures 3.4 and Figure 3.5).

The diversity of Amazonian amphibians remains under-described. In addition to a sampling gap, which is largely associated with the remoteness of some of its habitats (Azevedo-Ramos and Gallati 2002), taxonomic reviews and inventories are insufficient to account for the diversity and distribution of Amazonian amphibians. Among Amazonian salamanders, for instance, the percentage of undescribed species is estimated to be as high as 400%, relative to the current number of known species (Jaramillo *et al.* 2020). In the Brazilian Amazon, amphibian diversity estimates increased 40% within three years (Azevedo-Ramos and Gallati 2002, Avila-Pires *et al.* 2007). This has implications for both basic and applied science, including the list of threatened species (Peloso 2010). For instance, comprehensive analyses of widely-distrib-

Figure 3.4 Amphibian diversity in the Amazon basin. (A) Embryos of the Andean glassfrog *Nymphargus wileyi*. (B) Torrent frog, *Hyloscirtus staufferorum*. (C) Tiger-striped Monkey Frog, *Callimedusa tomopterna*. (D) Amazonian salamander, *Bolitoglossa* sp. Photos by Tropical Herping.



Threatened Amphibian Species

Data Sources: AmphibiaWeb, IUCN 2017.

Figure 3.5. Threatened species of amphibians globally. Note that numerous species from the highlands of the Amazon Basin are endangered. Source: AmphibiaWeb (2020).

uted Amazonian amphibians frequently reveal rampant cryptic diversity, uncovering many species of smaller ranges within what was once assumed to be a single, widely distributed species (Funk *et al.* 2012, Fouquet *et al.* 2007, Jaramillo *et al.* 2020, Vacher *et al.* 2020). Amphibian biodiversity patterns display considerable variation within the Amazon Basin, often driven by the combined impact of topography, hydrology, evolutionary history, and the ecology of local species (Fouquet *et al.* 2015). Amphibian groups such as the tree frogs, monkey frogs, and poison-arrow frogs are more diverse in the lowland rainforests, whereas others, such as glass frogs, harlequin toads, and marsupial frogs are more diverse in the Andean cloud forests (Frost 2021, Guayasamin *et al.* 2020). Rivers appear to function as barriers to some amphibian taxa (especially non-riparian species, Moraes *et al.* 2016), but not all (Gascon *et al.* 2000). Their impact on the distribution of lineages can be river-specific (Funk *et al.* 2007b, Ortiz *et al.* 2018, Ferreira *et al.* 2020) and depends on the ecology of the species (Fouquet *et al.* 2015). The uplift of the Andes and the resulting lowland geological dynamics may have influenced patterns of amphibian diversity in the Amazon, as supported by a study of shifts in species composition along river transects (Gaston *et al.* 2000). DNA-based studies support the idea that lowland Amazonian communities were part of a connected set of Neotropical ecosystems, which they repeatedly colonized more than 10 million years ago. Colonizing amphibians, especially from the Andes, contributed new lineages to adjacent areas (Santos *et al.* 2009).

To preserve the diversity of amphibians of the Amazon Basin is to maintain their key ecological roles, cultural value, unique evolutionary histories, and also a potential for bioprospection (*e.g.*, in species with potent skin alkaloids such as the poison dart frogs; Badio and Daly 1994, Daly 1995, Rodríguez *et al.* 2017). However, given their extreme vulnerability to habitat destruction, climate change, and infectious diseases, amphibians are often considered at higher risk of extinction relative to other groups of organisms (Schee-le *et al.* 2019, Stuart *et al.* 2004, Wake and Vredenburg 2008).

3.2.6 Diversity of reptiles

Reptiles are among the most diversified vertebrate groups on the entire planet. Currently, 11,341 species have been recorded, in 92 families and 1,206 genera (Uetz and Hosec 2020). However, even with several studies carried out in the Amazon in the last decades, the diversity of species continues to be underestimated given the frequent discovery of new cryptic species, demonstrating that we are still unaware of the real diversity of this group (*e.g.,* Oliveira *et al.* 2016). The Amazon rainforest registers 371 species, occupying an immense number of terrestrial and aquatic environments (Mittermeier *et al.* 2003, Avila-Pires and Ramalho 2019). Reptiles have intriguing patterns of diversity and distribution throughout the entire Amazon Basin, such as the well-known patterns of distribution and diversity along latitudinal gradients and the west to east gradient (Da Silva and Sites 1995, Guedes *et al.* 2018, Roll *et al.* 2017).

In addition, squamata reptiles show an intriguing pattern of variation in species richness along a north–south gradient that runs from eastern Ecuador to southeastern Peru. For example, some studies carried out in the northwestern Amazon indicate a greater diversity of species in relation to locations in the southeast Amazonian plain (*e.g.,* Da Silva and Sites 1995). Recently, estimates of species richness obtained from different sampling locations, as well as from specimens obtained from scientific collections, suggest a greater richness of snake species in the northwestern Amazon compared with the southern region (Rabosky *et al.* 2016). In addition, these and other results imply that the alpha diversity for Squamata distributed to the north of the Amazon can be up to 30% greater in relation to the communities in the south (Da Silva and Sites 1995, Duellman 2005).

3.2.7 Diversity of birds

The Amazon hosts the highest number of birds in the world. With at least 1,300 species, of which approximately 265 are endemic, the Amazon harbors approximately 38% of the Neotropic's approximately 4,000 birds (Nores 2000, Mittermeier *et al.* 2003). The true number of bird species in the Amazon could be much higher. Relatively recent molecular systematic studies have revealed that traditionally accepted species often group several genetically divergent lineages representing new cryptic species together (Milá *et al.* 2012). Bird diversity increases in proximity to the Andes. The topography and ecology change at an elevation of approximately 500 m, where many lowland bird species (~800) reach their upper elevational range, and many Andean birds reach their lowest elevational range (Nores 2000, 2011). For several decades, scientists have been trying to understand the geographic structure of bird communities and the underlying causes for observed patterns of speciation (*e.g.*, Haffer 1969, Bates 2001, Pomara *et al.* 2014, Ribas and Aleixo 2019).

The evolution of Amazonian birds is a complex process, but molecular systematics and phylogeographic studies suggest that many avian lineages diversified recently during the late Tertiary and early Quaternary (Weir 2006, Aleixo and Rossetti 2007, Silva *et al.* 2019). This period coincides with large landscape changes (*e.g.*, Colinvaux 1993, Haffer 1993, Bush 1994, Marroig and Cerqueira 1997). It appears, during the Pliocene, ancestral bird faunas occupied mostly upland forested habitats in the northern and western Amazon. After a series of interactions between climate-driven dynamics and riverine barriers, avian lineages started separating on opposite sides of the region, Negro and Madeira rivers (the most ancient rivers in the Basin). These changes in climate and connectivity affected bird populations differently, depending on their ecological requirements and degree of habitat specialization. As a result of this processes, currently, the wetter western Amazon contains older and richer bird faunas compared with the dryer eastern Amazon (Silva *et al.* 2019). However, knowledge of the evolution of Amazonian birds is a complex process and data are still fragmented. More sampling is needed to understand regional patterns of bird species richness and community composition in the Amazon (Oliveira *et al.* 2017).

3.2.8 Diversity of mammals

The Amazonian region harbors one of the richest mammalian faunas of the world, with approximately 140 genera and 425 species (Mittermeier *et al.* 2003). Amazonian mammals account for approximately one-third of all South American mammalian diversity, approximately 1,260 species (Bonvicino and Weksler, 2012). In addition, several locations in the Amazon have the highest alpha-diversity of non-volant mammals anywhere on Earth (Peres, 1999, da Silva *et al.* 2015). However, the number of species at any single locality in the Amazon significantly varies depending on forest types and habitat diversity. Mammal communities in seasonally flooded (*várzea*) forests, for example, can be considered relatively impoverished when compared with neighboring *terra firme* forests, although density and biomass can be significantly higher in *várzea* than in *terra firme* (Peres 1997, Haugaasen and Peres 2005). Endemism is also very high, with 10 endemic genera and 144 species of mammals (34% of total) found only in the Amazon (Pires *et al.* 2000, Solari *et al.* 2012). This impressive mammalian diversity is not distributed equally among orders. The high level of endemism of Amazonian mammal species is due mainly to the input of three orders, marsupials, rodents, and primates, which together comprise approximately 80% of all endemic species (Voss and Emmons 1996, Paglia *et al.* 2012).

Despite these figures, the mammalian fauna of this vast region is still under-sampled, and there are not enough exhaustive surveys of mammals. As a result, the spatial turnover of species assemblages at different scales remains poorly understood (Voss and Emmons 1996, Peres 1999, Solari *et al.* 2012). Based on mammal inventories carried out throughout the Amazon, it has been suggested that mammalian communities in the western Amazon are the most diverse in the region, the Neotropics, and probably the world. Explanations for this pattern include present-day ecological factors such as climate, habitat, and topographical heterogeneity; primary productivity; and ecosystem dynamics (Voss and Emmons 1996, Peres 1999; Machado *et al.* 2019). Mammals are considered well-known because the rate at which new species are discovered is low compared with other groups. However, in recent years several new species have been described and new records have extended the geographical ranges of some species by hundreds of kilometers (Patterson 2001, 2020). We are still learning about the fascinating diversity of Amazonian mammals, and this knowledge is critical for the conservation of the Amazon region.

The Amazon has experienced a dynamic process of transformation throughout its history, including marine transgressions and abrupt changes in the flow of its water bodies. The creation of geographical barriers, such as rapids and streams, has allowed many species to prosper and others to disappear. Among them, aquatic mammals play an important role. The dolphins of the genus *Inia* moved from the Atlantic to the center of the continent in Bolivia, where they were isolated about 3.1 million years ago by the Madeira River (Hollatz *et al.* 2011), while others dispersed throughout the Amazon and the Orinoco region. Currently, only the presence of the species *Inia geoffrensis* is recognized with two subspecies: *Inia geoffrensis geoffrensis* distributed in the Amazon and Orinoquia, and *Inia geoffrensis boliviensis* in Bolivia and the Madeira River (Da Silva *et al.* 2018). However, there is evidence to suggest that the Bolivian unit may be a different species (*Inia boliviensis*), and in the Tocantins/Araguia complex in Brazil *Inia araguiaensis* (Hrbek *et al.* 2014). Similarly, approximately 2.5 million years ago, the ocean level rose approximately 150 meters and generated another transgression of the sea into the Amazon, promoting the entry of another dolphin of the genus *Sotalia*. This species adapted to freshwater conditions, evolving to *Sotalia fluviatilis* approximately 1.2 million years ago. Also, there is evidence to suggest that during the Pliocene, some 4.5 million years ago, there was a displacement of manatees from the Atlantic to the Amazon, giving rise to the only species of freshwater manatee, *Trichechus inunguis*, distributed in Brazil, Colombia, Peru, and Ecuador (Domning 1982). Another important group of aquatic mammals in the Amazon are the otters; the giant river otter (*Pteronura brasiliensis*) and the Neotropical otter (*Lontra longicaudis*), whose origin seems to be associated with the geological, hydrological, and climatic changes that the region experienced during the Pliocene-Pleistocene.

3.2.9 Diversity of parasites and pathogens (and their interactions with mammalian hosts)

If the biodiversity of animals, fungi, and plants in the Amazon is still poorly known, much less can be said about the biodiversity of pathogens and parasites. Despite accounting for one-third to over half of the species on Earth (Poulin 2014), these organisms are usually ignored in biodiversity inventories and conservation studies (Gómez and Nichols 2013). Most of the current knowledge is highly biased to parasites that cause human, domestic animal, or plant diseases (Gómez and Nichols 2013). Nevertheless, parasites and pathogens play an important role at individual, population, and ecosystem levels (Wood and Johnson 2015), such as modulating the immunity of hosts and the dynamics of their populations, altering the composition of ecological communities, and modifying trophic interactions, including predation rates and nutrient cycling. These processes have complex effects, both direct and indirect, which may include cascade effects and co-extinctions, whose implications are not yet completely understood (Strona 2015).

Despite the significance of parasite biodiversity, the actual richness of most parasitic groups remains largely unknown. When accounting for the biodiversity of mammal parasites in the Amazon region, we found that from the 425 wild mammals, only 185 species have been studied regarding their interactions with parasites. Brazil is the country that published the largest number of studies on mammal-parasite interactions, followed by Peru, French Guiana, Bolivia, Venezuela, Guyana, Ecuador, and Colombia. The mammal species with the highest richness of studied parasites are the marsupial *Didelphis marsupialis*, the bat *Carollia perspicillata*, and the primates *Sapajus apella* and *Saimiri sciureus*. However, most of those studies report interactions with a single parasite species; studies investigating the community composition of parasites or co-infections are rare (Conga *et al.* 2014). Protozoans are the parasite group with the largest number of studies (84 publications), but are not the group with the highest richness of species. The parasite group with the highest number of species reported interacting with wild mammals are helminths (77 species), arthropod ectoparasites (65 species), viruses (62 types), protozoans (29 species), bacteria (12 species), and fungi (seven species).

Table 3.2 Most studied parasite and pathogen species in the Amazon.

Parasite Groups	Most Studied Species	References
Virus	*Rabies lyssavirus,* Laguna negra orthohantavirus, Simian foamy virus	Deem and Emmons 2005, da Rosa *et al.* 2012, Carnieli Jr *et al.* 2013, Costa *et al.* 2013, Favoretto *et al.* 2013, Kobayashi *et al.* 2013, Muniz *et al.* 2013, de Barros Lopes *et al.* 2014, Oliveira *et al.* 2015, Pereira *et al.* 2017
Arbovirus	*Changuinola, Marituba, Mayaro, Oriboca, Oropouche*	Leduc *et al.* 1981, Figueiredo *et al.* 1988, de Thoisy *et al.* 2003, Silva *et al.* 2013, Silva *et al.* 2014, Hang *et al.* 2014, Nunes *et al.* 2018, Nunes *et al.* 2019
Bacteria	*Leptospira interrogans, Mycobacterium leprae*	Deem and Emmons 2005, da Silva *et al.* 2018, Stefani *et al.* 2019, dos Santos Medeiros *et al.* 2020
Helminth	*Dipetalonema gracile, Toxocara canis, Trypanoxyuris minutus, Trypanoxyuris trypanuris*	Hugot 1985, Bain *et al.* 1986, Tantalean *et al.* 1990, Hugot *et al.* 1996, Stuart *et al.* 1998, Hugot 1999, Noronha *et al.* 2002, Deem and Emmons 2005, Vieira *et al.* 2008
Protozoa	*Trypanosoma cruzi, Trypanosoma rangeli, Trypanosoma cruzi marinkellei, Trypanosoma dionisii, Toxoplasma gondii*	Deane 1961, Deane and Damasceno 1961, Ayala 1964, Baker 1972, Miles *et al.* 1981, Miles *et al.* 1983, Lanham *et al.* 1984, Póvoa *et al.* 1984, Carrasco *et al.* 1996, Ziccardi and Lourenço-de-Oliveira 1997, Stuart *et al.* 1998, de Thoisy *et al.* 2003, Deem and Emmons 2005, Dubey *et al.* 2007, Demar *et al.* 2008, Lisboa *et al.* 2008, Roque *et al.* 2008, da Silva *et al.* 2009, Marcili *et al.* 2009a, Marcili *et al.* 2009b, Marcili *et al.* 2009c, Ortiz *et al.* 2009, Cavazzana *et al.* 2010, Lewis *et al.* 2011, De Araujo *et al.* 2013, Monteiro *et al.* 2012, Roque *et al.* 2013, Acosta *et al.* 2014, Vitaliano *et al.* 2014, da Costa *et al.* 2015, Jansen *et al.* 2015, Lima *et al.* 2015, da Costa *et al.* 2016, dos Santos *et al.* 2017, Rodrigues *et al.* 2017, Jansen *et al.* 2018, Barros *et al.* 2019, Filgueiras *et al.* 2019, Pérez *et al.* 2019, Rodrigues *et al.* 2019, McClean *et al.* 2020
Ectoparasite	*Amblyomma ovale, Amblyomma naponense, Amblyomma geayi, Amblyomma cajennense, Amblyomma nodosum*	Stuart *et al.* 1998, Labruna *et al.* 2002a, Labruna *et al.* 2002b, Robbins and Deem 2002, Zerpa *et al.* 2003, Deem and Emmons 2005, Labruna *et al.* 2005, Robbings *et al.* 2009, Martins *et al.* 2013, Martins *et al.* 2014, Soares *et al.* 2015, Witter *et al.* 2016, Furtado *et al.* 2017, Zimmermann *et al.* 2018, Gruhn *et al.* 2019, Peckle *et al.* 2019
Fungi	*Histoplasma capsulatum, Pneumocystis carinii*	Lainson and Shaw 1975, Arias *et al.* 1982, Naiff *et al.* 1985, Naiff *et al.* 1996, Hugot *et al.* 2003

From those, 38 viruses, 16 arboviruses, 11 bacteria, nine helminths, 19 protozoans, one ectoparasite, and seven fungi are known to be zoonotic and cause disease in humans. The most studied parasites infecting wild mammals in the Amazon region are the protozoans *Trypanosoma cruzi* (the causative agent of Chagas disease in humans), *Plasmodium brasilianum*, *Trypanosoma cruzi marinkellei*, *Trypanosoma rangeli*, the virus *Rabies lyssavirus* (the causative agent of rabies in humans), and the ectoparasite *Amblyomma cajennense* (Table 3.2).

Concerning arthropod-borne viruses (or arboviruses), 27 different species have been recorded as infecting wild mammals in the Amazon. From those, 16 are known to be zoonotic, including the viruses Caraparu, Changuinola, Dengue, Guama, Mayaro, Marituba, Murutucu, Oriboca, Oropouche, Piry, Saint Louis, Tacaiuma, and Yellow fever. It is important to emphasize that in the Amazon region some of these zoonotic agents are also shared with domesticated mammal species such as pets and cattle, and that other zoonotic pathogens have already been identified in domesticated animals (e.g., Eastern Equine Encephalitis Virus and West Nile Virus). These domesticated species can play an important role in the transmission cycle of zoonotic agents (Johnson *et al.* 2020), especially when in high densities (e.g., livestock production), functioning as amplifying hosts and intermediating transmission to humans and wild animals. Given recent concerns about the risk of an emerging pandemic originating in the Amazonian region (Vale *et al.* 2021), current increasing rates of deforestation, the loss and homogenization of biodiversity, and increasing social vulnerabilities are major concerns. This, added to the gap of knowledge about the biodiversity of host-parasite interactions, elucidates the need for understanding and building resilience to emerging diseases as a top societal challenge and research priority.

3.3 Outstanding Ecological Processes and Adaptations in Terrestrial and Aquatic Ecosystems

3.3.1 Plant-animal interactions

Plant-animal interactions are a central ecological process in Amazonian forests, without which these forests would cease to exist: 80–90% of trees obligately rely on animals for seed dispersal (Gentry 1982, Hawes *et al.* 2020), and as many as 98% of plants obligately rely on animals for pollination (Bawa 1990). Animal dispersers are attracted to seeds by a wide variety of plant strategies, and birds, bats, mammals, fish, and insects are all important dispersers responding to and selecting for different plant strategies for attraction (*e.g.*, Howe and Smallwood 1982). Consumptive effects generate diversity through coevolutionary arms-races and control plant and animal biodiversity on ecological and evolutionary time scales. These networks of mutualists and consumers regulate all aspects of Amazonian forests, and are responsible for their composition, species regulation, recovery from disturbance, and the generation of biodiversity. Changes to species interactions can have cascading effects on Amazonian ecosystem function and the services they provide humanity, as briefly discussed below.

Seed dispersers and pollinators interact with plants, form mutualistic networks, and form the very architecture of Amazonian biodiversity (Bascompte and Jordano 2007). Seed dispersal moves seeds away from parent trees, cleaning them of pulp and in many cases physiologically altering them, all of which improve survival and increase genetic diversity (Howe and Smallwood 1982, Hardesty *et al.* 2006). Seed disperser communities are exceptionally complex (Jordano *et al.* 2007), and plant-disperser networks are comprised of many different modules of differing kinds of dispersers (Donatti *et al.* 2011), underscoring their importance of maintaining biodiversity in these systems (Kakishima *et al.* 2015). Vast areas of the Amazon are seasonally flooded, and fish have been shown to be critical dispersers in these forests and link terrestrial and aquatic processes (Goulding 1983, Correa *et al.* 2015a). Pollination networks in Amazonian forests are highly diverse and complex, include a wide variety of invertebrates and vertebrates, and form the basis of reproduction in the perpetuation of Amazonian forests (Bawa 1990, Bascompte and Jordano 2007). Pollinator networks are often highly specialized and are built with modules of interacting species with low redundancy, underscoring the role of pollinator biodiversity and conservation on overall Amazonian biodiversity and ecosystem services (Kremen *et al.* 2007, Olesen *et al.* 2007).

Trophic interactions are equally important, locking animals into networks of herbivory on leaves, seeds, and roots, with high degrees of specialization. Plant-herbivore coevolutionary interactions have led to the evolution of high species diversity by locking groups of organisms in evolutionary arms races of attack and defense (Ehrlich and Raven 1964), and have led to a spectacular diversification in Amazonian plant functional traits and chemical defenses that not only regulate and generate forest diversity, but also provide critical services for humanity (Coley and Barone 1996, Fabricant and Farnsworth 2001, FAO *et al.* 2011). Herbivore effects on plants depend on both geology and climate, and trade-offs in these interactions have generated landscape-level diversification of tropical trees (Fine *et al.* 2004, Fine *et al.* 2013). Plant-herbivore interactions have emerged as the key component in maintaining diversity in tropical forests, with frequency- and density-dependent effects at multiple scales (Janzen 1970, Harms *et al.* 2000, Terborgh 2012). All of these plant-animal interactions are embedded in food-webs of consumptive interactions, which in turn regulate them in Amazonian ecosystems, with direct regulation by predation, and indirect mutualisms arising from trophic cascades (Schmitz 2008, Terborgh and Feely 2009).

Plant-animal interactions are at high risk from multiple forms of human-caused change (*e.g.*, Sales *et al.* 2020, 2021). Disruptions to plant-animal interactions can have rapid effects on forest community composition, which has long-term consequences (Terborgh *et al.* 2001), changing forest composition as well as ecosystem function and services (Morris 2010). Defaunation has cascading effects on Amazonian forests through the direct effects of hunting and indirect effects of anthropogenic disturbances, particularly affecting large-bodied vertebrates (Bodmer *et al.* 1997). Defaunation affects all plant-animal interactions, especially disperser and seed predation networks, with significant consequences for Amazonian tree diversity (Kurten 2013, Peres *et al.* 2016); ecosystem function and services, particularly carbon storage (Markl *et al.* 2012, Bello *et al.* 2015); nutrient cycling (Stevenson and Guzmán-Caro 2010, Doughty *et al.* 2016); and even biogeography (Doughty *et al.* 2016). Deforestation and forest fragmentation can have effects beyond simple removal of trees, with effects cascading through pollination (Wirth *et al.* 2008, Barlow *et al.* 2016, Lister and García 2018), dispersal (Laurance *et al.* 2006, Markl *et al.* 2012, Caughlin *et al.* 2014, Hawes *et al.* 2020), and consumptive networks (Terborgh 2013), fundamentally changing the ecological interactions that maintain and generate Amazonian biodiversity. Plant-animal interactions are particularly vulnerable to climate change effects, both directly through disruption of plant-animal interaction networks due to differential responses to climate among components (Primack *et al.* 2009, Salcido *et al.* 2020), and indirectly by exacerbating the effects of defaunation and forest degradation (Valladares *et al.* 2006, Barlow *et al.* 2016). An overwhelming and central result from the study of Amazonian forests is that intact plant-animal interaction networks are essential for the resilience of forest biodiversity to anthropogenic changes, and for the recovery and restoration of Amazonian systems.

3.3.2 Flood pulses and nutrient flow

Aquatic ecosystems in the Amazon are a complex mosaic of habitats influenced by flood pulses and by the pattern of nutrient flow. This has generated areas with high and low productivity, which have promoted complex adaptation processes in aquatic organisms. Fish are undoubtedly one of the most relevant cases, supporting large biomass in highly productive rivers (white-water), such as the Amazon, Madeira, Caquetá/Japurá, Putumayo, and Purus, and low biomass but high species richness in rivers of black- and clear-waters. In the latter, the fish depend more on external sources of food (fruits, seeds, insects) or on trophic subsidies provided by migratory fishes (see Section 3.3.3). Given the transparent conditions in clear- or black-waters, fish usually develop intense colors with an important function for reproduction (Borghezan *et al.* 2021).

Many species that live in floodplains have special adaptations to withstand low oxygen levels and high temperatures during periods of drought (Junk *et al.* 1983, Val 1995, Val and Almeida-Val 1995, Val *et al.* 2015). However, other species choose to perform lateral migrations towards main channels for reproductive purposes, spawning in the main channels and then returning to lakes and small tributaries. These fish are predominantly from the Prochilodontidae and Curimatidae families. Species such as the pirarucu (paiche, *Arapaima gigas*), which are apparently sedentary, build nests at the bottom of lakes and reproduce during the low water season. When the water level rises, they make small lateral migrations towards flooded forest, where the males exercise parental care of their young (Castello 2007).

Large aquatic carnivores, such as the Amazon river dolphin (*Inia geoffrensis*), sometimes follow fish migrations, ensuring permanent and abundant access to prey. In general, the females seem to be more resident and are associated with systems of lakes and confluences where they take care of their young, while males make long migrations in search of food and reproductive options (Trujillo *et al.* 2018). In adaptive terms, the Amazon river dolphin has developed a better ability to search for fish in the flooded forest than its sympatric species, the gray dolphin (*Sotalia fluviatilis*). The cervical vertebrae of their neck are not fused, allowing them to move their heads, which, combined with a long snout, allows them to catch benthic or pelagic fish that hide under macrophytes or among submerged vegetation. Likewise, a low dorsal fin and pectoral fins with great movement capacity allow them to move very well in the flooded forest. Something similar occurs with giant otters (*Pteronura brasiliensis*), which make up family groups of between 6 and 14 individuals. They are mainly located in tributaries and lagoons and have more or less well-defined territories during the low water period, but when the water level increases, the fish disperse in the flooded forest and the size of the territory increases.

During periods of low water, large stretches of beaches are exposed and are the ideal habitat for the massive spawning of several species of turtles, especially of the genus *Podocnemis*, such as the Giant Amazon River Turtle (*Podocnemis expansa*) and Yellow-Spotted River Turtle (*Podocnemis unifilis*). The reproductive success of these species depends, to a great extent, on the characteristics of the beach, mainly the type of sediment and the height at which the nests are dug, as there are frequent rises in water levels that can affect nests in lower parts. Another species that has adapted to flood pulses in the Amazon are jaguars (*Panthera onca*), which were thought to move to non-flooded areas during these periods. Recent studies show that in areas such as Mamirauá in Brazil, they can spend up to three months living in the treetops, feeding primarily on sloths, alligators, and even giant otters (Ramalho 2012, Alvarenga *et al.* 2018).

3.3.3 Fish migrations

Migratory fishes play important ecological roles in Amazonian aquatic food webs, providing crucial subsidies from one component of the ecosystem to the other, either as predators or prey, or as engineers or seed dispersal agents. Therefore, modification or disruption of their migratory patterns by overharvesting, impoundment, or habitat degradation is likely to profoundly alter ecosystem processes by modifying trophic cascades, primary production, detrital processing, and subsidies transfer over wide spatial scales (Flecker *et al.* 2010, Barthem *et al.* 2017, Anderson *et al.* 2018).

Amazonian goliath catfish of the genus *Brachyplatystoma* perform the world's longest known freshwater migration. One species, *B. rousseauxii*, uses almost the entire length of the Amazon Basin in a round trip migration of up to ~12,000 km between its spawning areas in the Andean piedmont of Bolivia, Colombia, Ecuador, and Peru, to its nursery in the estuary in Brazil (Barthem and Goulding 1997, Barthem *et al.* 2017, Duponchelle *et al.* 2016, Hauser *et al.* 2020). This exceptional migration involves natal homing, a behavior seldom observed in freshwater, but common in species migrating between the sea and rivers, such as salmon. In this process, adult fish usually return to the watershed where they were born either in the upper Madeira (Duponchelle *et al.* 2016) or in the upper Amazon (Hauser *et al.* 2020). Together with river dolphins, goliath catfish are the apex predators of Amazonian rivers (Barthem and Goulding 1997) and several species are overharvested (Barthem *et al.* 1991, Petrere *et al.* 2004, Agudelo *et al.* 2013). As demonstrated in both marine and freshwater ecosystems, top predators play essential ecological functions and the depletion of their populations can entail profound modifications of ecosystems through trophic cascades (Baum and Worm 2009, Chase *et al.* 2009, Frank *et al.* 2005, Persson *et al.* 2007). Similar cascading effects are expected with the decline of the large goliath catfish community in the Amazon Basin (Angelini *et al.* 2006, Lima 2017), which could be further accentuated by their exceptional migratory behavior (Borer *et al.* 2005).

Fish migrations, and in particular the movements of detritivorous fishes, also play crucial ecological roles in nutrient transport, with important consequences on local food web dynamics. Fishes of the family Prochilodontidae (*Prochilodus* and *Semaprochilodus*), which feed on detritus, algae, and associated microorganisms (Bowen 1983), indeed perform complex, large-scale migrations from nutrient-poor tributaries (black- or clear-waters) during the low water period to the rich floodplains of white-water tributaries for spawning and feeding during high waters (Ribeiro and Petrere 1990, Vazzoler and Amadio 1990, Vazzoler *et al.* 1989). Their movements between different river systems connect food webs over large spatial scales and result in important energy and biomass transfer into oligotrophic waters, where these species are preyed upon by large piscivores that could normally not support high population densities without these subsidies (Hoeinghaus *et al.* 2006, Winemiller and Jepsen 1998). Although this phenomenon has mainly been studied in Prochilodontid fishes, flows of primary production from nutrient-rich white-water rivers into clear- or black-water rivers by migratory detritivorous species is likely widespread in the Amazon Basin, as many other migratory characids, such as *Anodus* spp., *Brycon* spp., *Colossoma macropomum*, *Leporinus* spp., *Mylossoma* spp., *Triportheus* spp. spawn and grow exclusively in white-water, but can live in any water type as adults (Lima and Araujo-Lima 2004). Another striking case is the annual migration of the juvenile pencil catfish, *Trichomycterus barbouri* (~3 cm), which consists of hundreds of thousands of individuals moving from their nursery area in the downstream Béni River to its upper reaches hundreds of kilometers upstream (Miranda-Chumacero *et al.* 2015). This migration provides a source of food for fish, water birds, reptiles, and human populations along the way.

Many Amazonian migratory fishes have co-evolved a mutually beneficial relationship with the forest. During the high-water season, migratory fishes invade the flooded forest to feed on fruit that falls into the water, dispersing seeds over large distances while improving their germination process (Goulding 1980, Correa and Winemiller 2014, Correa *et al.* 2015a). Most of the approximately 150 known frugivorous fish species in the Neotropics, belonging to 17 families and 6 orders, also occur in the Amazon Basin (Horn *et al.* 2011). They can consume at least 566 species of fruits and seeds from 82 plant families, thereby contributing to their spatial distribution and biodiversity (Correa *et al.* 2015a). Because commercial fisheries primarily target large-bodied species, which can disperse seeds of a broader size range and of a higher diversity of plants, overharvesting could threaten not only fruit-eating fish populations, but also the biodiversity and conservation of the flooded forest (Correa *et al.* 2015b).

3.3.4 Environmental variation and adaptation of organisms

Of the 7 million km^2 covered by the Amazon region, 800,000 km^2 are aquatic ecosystems. The interaction between land and water responds to a delicate climatic gear that is responsible for the flood pulse (Junk *et al.* 1989). This is undoubtedly one of the most important and relevant environmental processes in the Amazon, since it generates variations of up to 15 m in the vertical plane and thousands of kilometers of flooding in the lateral plane. This clearly marks a low-water period and a high-water period, with transition periods throughout the year. This cycle, repeated for thousands of years, has generated exceptional adaptation processes by fauna and flora. A good part of the vegetation is adapted to being submerged for several months and synchronizing its fruiting processes in high waters as a dispersal strategy. Likewise, during this period, the proliferation of macrophytes and large patches of aquatic vegetation serve as a refuge for fish and other organisms and provides food for species such as manatees and capybaras (Parolin *et al.* 2004, Piedade *et al.* 2010, Junk *et al.* 2011).

Changes in the water level also generate a mechanism that triggers the lateral migration of many species, including fish, dolphins, and manatees (Cox-Fernandes 1997, Martin and da Silva 2004, Arraut *et al.* 2010). In the case of dolphins, in high waters, they disperse into the flooded forest, tributaries, and lagoons in search of food, but when the water level begins to decrease, gray dolphins (*Sotalia fluviatilis*) move to the main rivers and later Amazonian dolphins (*Inia geoffrensis*) do as well to avoid being trapped in bodies of water with a low supply of food. Shallow waters represent the time of greatest availability of food in the main rivers. With the contraction of the entire system, the fish are contained in a smaller space and dolphins take advantage of this to feed. This increase in energy allows reproduction to be synchronized with the season. The young are born 13 months later, also in periods of low water levels. In contrast, manatees benefit from higher macrophyte production in high water periods, while in summer they must browse submerged logs for algae and subsist on body fat reserves.

3.4 Genetic Plasticity and Molecular Diversity

Because species delimitation is based on genetic variation, natural selection, and adaptation (Sexton *et al.* 2009), species richness is widely regarded as a fundamental measure of biodiversity at the general level (Gotelli and Colwell 2001). Patterns of genetic variation in species also represent a vital but often underestimated component of Amazonian biodiversity; phylogenetic diversity assesses the evolutionary and cumulative distinctiveness within and between areas and taxa (Antonelli *et al.* 2018a). Phylogenetic diversity measures the total amount of evolution per lineage over time among all members of a clade or area (Tucker *et al.* 2017). In general, this has been shown to provide a better estimate of feature divergence than species richness alone (Forest *et al.* 2007).

Although many groups of organisms are widely distributed in tropical regions, the detailed pattern of variation in species (Costa and Magnusson 2010), including spatial, genetic, and morphological variation, and their genetic structure have recently been documented, corresponding to several independent evolutionary units (Ribas *et al.* 2012, Schultz *et al.* 2017). Genetic diversity of terrestrial mammals and amphibians is 27% higher in tropical areas, and disturbed habitats have less genetic diversity compared to undisturbed areas (Miraldo *et al.* 2016). Well-sampled molecular phylogenies have recently been developed to reveal the evolution of tropical biota (Dexter *et al.* 2017, Eiserhardt *et al.* 2017). Molecular sampling at the intraspecific level (subspecies and populations) has significantly advanced in the Neotropics (Antonelli *et al.* 2018b). According to the analysis of dated molecular phylogenies, it has been shown that some Neotropical regions may be more permeable to immigrating lineages than others. Furthermore, the intrinsic differences between taxonomic groups (such as dispersal capacity) may allow some lineages to colonize new regions (Antonelli *et al.* 2018b), despite niche conservatism (Crisp *et al.* 2009), and others support adaptations to ecological changes (Simon *et al.* 2009, Trujillo-Arias *et al.* 2017). However, for most taxonomic groups of the Amazon, knowledge about biotic exchanges and dispersal histories remains surprisingly poor, and it is not understood which regions served as primary sources and sinks of biodiversity, defined as providers and recipients (Antonelli *et al.* 2018b). It has been concluded that the Amazon is the main Neotropical diversity source of angiosperms, ferns, snakes, birds, mammals, and frogs for other regions, providing >2,800 lineages (63% of all dispersal events), being approximately 4.6 times the second most important source of diversity (Antonelli *et al.* 2018b, Figure 3.6).

As it is known, both the western and central Amazon have the highest species richness of tree communities (ter Steege *et al.* 2003, Chave *et al.* 2007) and, therefore, the highest phylogenetic diversity, but the lowest mean nearest taxon distance (Honorio Coronado *et al.* 2015). The mean pairwise phylogenetic distance between species is correlated with how evenly taxa are distributed among the three principal angiosperm clades (Magnoliids or Dicots, Monocots, Eudicots) and are both the highest in the western Amazon. Finally, seasonally dry tropical forests and forests on white sands have low phylogenetic diversity (Fine *et al.* 2010, Honorio Coronado *et al.* 2015).

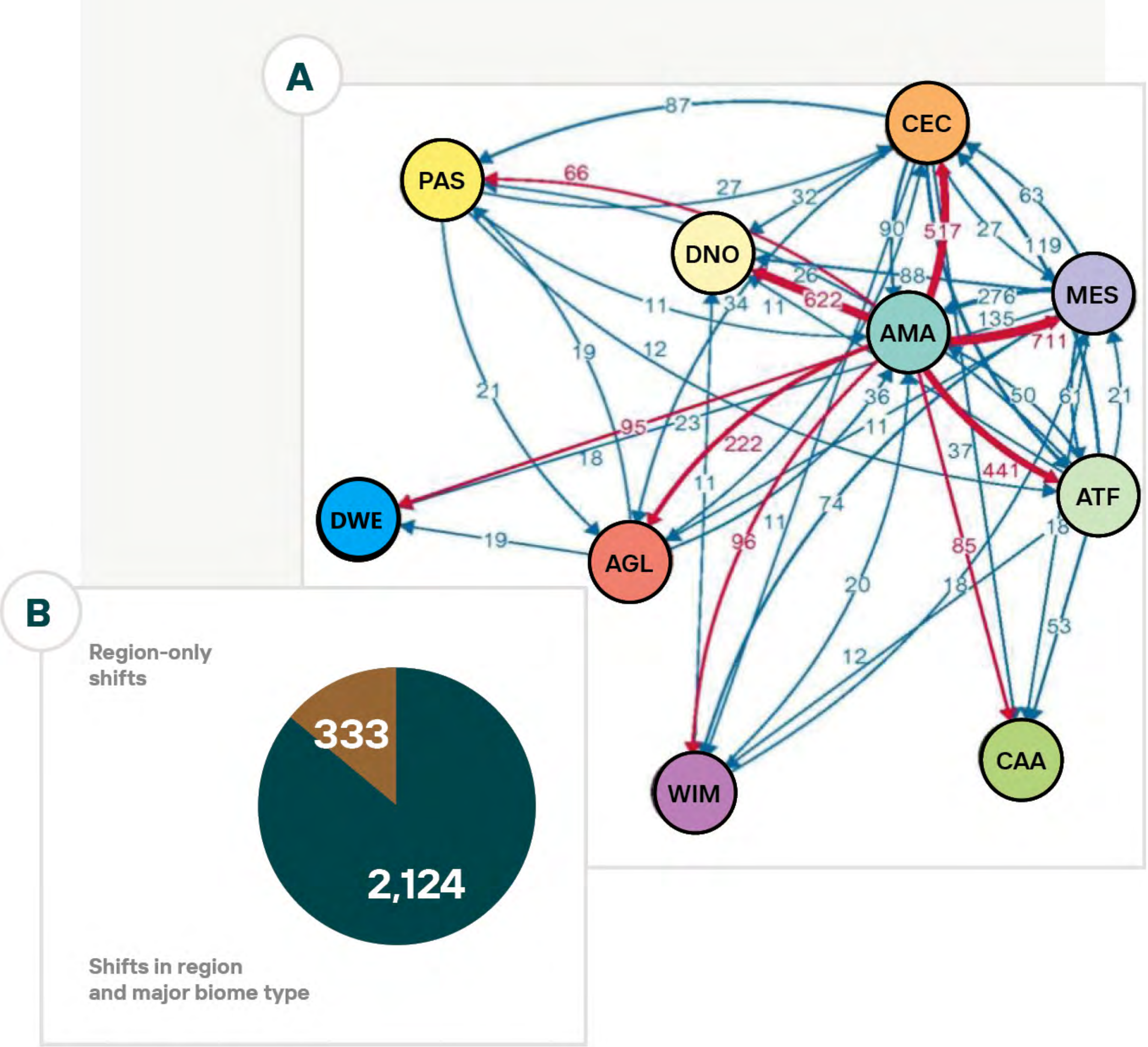


Figure 3.6 The Amazon as the main source of biodiversity lineages in the Neotropics (Antonelli *et al.* 2018b). A) Biotic interchange among Neotropical regions estimated from dated molecular phylogenies. Arrows indicate the direction and number of dispersal events, with line thickness proportional to the number of events. Only connections with more than 10 events are shown. The position of the circles in the layout reflects the biotic connection between regions. Dispersal events out of the Amazon are highlighted in red. AGL, Andean Grasslands; AMA, Amazonia; ATF, Atlantic Forests; CAA, Caatinga; CEC, Cerrado and Chaco; DNO, Dry Northern South America; DWE, Dry Western South America; MES, Mesoamerica; PAS, Patagonian Steppe; WIM, West Indies. B) Number of nonambiguous dispersal events associated with shifts in major biome types compared with shifts to other regions within the same biome type.

In the face of environmental change and impacts, populations with reduced genetic diversity may be less capable of responding (Whitman and Agrawal 2009), and thus more vulnerable to fragmentation processes and local extinctions (Spielman *et al.* 2004). This genetic diversity has been proposed as a mechanism to survive in heterogeneous or changing environments, such as the tropics (Lande 2014). A classic example regarding the constant changes in oxygen content in Amazonian waters is the development and reversal of various morphological traits in fishes under hypoxic conditions (Almeida-Val *et al.* 2006, Fernández-Osuna and Scarabotti 2016). Furthermore, the ability of various lineages to establish themselves in the western and southern Amazon may also be related to high rates of alteration and turnover in the region (Quesada *et al.* 2012, Marimon *et al.* 2013, Baker *et al.* 2014).

3.5 Functional Diversity

Functional diversity, or the value, range, and distribution of functional traits in a given community, plays a key role in the generation and maintenance of biodiversity and ecosystem processes. Functional diversity depends on the variability of trait values of all species present, both within and between species, and on the extent of overlap of functional niches (Petchy and Gaston 2006, Díaz *et al.* 2007). Functional traits (Chapin *et al.* 2001, Violle *et al.* 2007) mechanistically link species to their effect on the ecosystems in which they live. For example, functional traits affect species competitive ability and coexistence (Kraft *et al.* 2008, Guilherme *et al.* 2019), invasion ability (Miranda-Chumacero *et al.* 2012, Van Damme *et al.* 2015), community and ecosystem structure and function (Bueno *et al.* 2013, Sobral *et al.* 2017), adaptations along environmental gradients (Asner *et al.* 2014a, von May *et al.* 2017, Santos *et al.* 2019), and resistance to disturbance and environmental change (Arévalo-Sandi *et al.* 2018, Arantes *et al.* 2019, Hooper and Ashton 2020).

Environmental conditions act as filters, determining functional diversity patterns in the Amazon Basin, selecting species exhibiting similar morphological, behavioral, or reproductive traits. For example, structurally, less complex environments (*e.g.,* savannah) harbor more species of smaller ants, with smaller mandibles and larger eyes. In more complex forested environments, there are more ant species of larger size, with larger mandibles and smaller eyes. Thus, the morphological composition of ground-dwelling ant assemblages corresponds to environmental complexity, suggesting that certain ant characteristics offer ecological advantages to particular species in particular habitats (Guilherme *et al.* 2019). Tree foliar chemistry provides another example of functional diversity varying with environmental conditions. Structural and defense compounds display striking diversity in the Amazon, and chemical portfolios of tree canopies dramatically shift along elevation and soil fertility gradients (Asner *et al.* 2014b). Likewise, the diversity of functional traits in fish communities, such as feeding strategies, life histories, migratory behaviors, and habitat use, is positively correlated with forest cover in river floodplains (Arantes *et al.* 2019). Accordingly, the environment influences functional diversity, and as habitat loss from deforestation proceeds, the suite of functional traits found in fish communities is highly compromised.

The Amazon is among the most functionally diverse regions on Earth for a number of taxa (*e.g.,* fish: Toussaint *et al.* 2016; plants: Wieczynski *et al.* 2019; amphibians: Ochoa-Ochoa *et al.* 2019). Taxonomic and functional diversity are often decoupled, and for some taxonomic groups, functional diversity is considerably higher in the Amazon than what would be expected from taxonomic diversity. Freshwater fish represent one striking example (Toussaint *et al.* 2016), and different hypotheses have been advanced to explain the tremendous functional diversity of freshwater fishes throughout the Neotropics (Albert *et al.* 2020). The Neotropics host approximately 40% of the world's freshwater fish species, yet this same region hosts more than 75% of fish functional diversity. Freshwater functional diversity in Amazon includes incredible variation in body form and trophic ecology, ranging from suckermouth wood-eating catfish (*e.g., Cochliodon, Panaque* spp) with teeth and jawbones specialized for gouging submerged tree trunks, to electric fish with smaller eyes living in turbid waters (Gymnotiformes), to migratory frugivores with molar-like teeth that can be important seed predators as well as seed dispersal agents (*e.g. Colossoma, Piaractus*; Correa *et al.* 2015a), to elongated vampire catfish that feed on blood in the gills of other fishes, *Vandellia* (Albert *et al.* 2020).

Functional diversity explains biological interactions and how organisms can drive crucial ecosystem processes. For example, trophic diversity, an important functional trait, influences how species can influence ecological processes such as predator-prey interactions, seed dispersal, carbon sequestration, and biogeochemical cycling, all critical functions in Amazon aquatic and terrestrial ecosystems. Moreover, species diversity per se can be a strong driver of ecosystem function. For example, in the mixed forest-savanna landscapes of the Rupununi region of Guyana, mammal species richness appears to be strongly correlated with carbon cycling (Sobral *et al.* 2017). Interestingly, concentrations of soil carbon and carbon storage in soil and trees are highest at sites with the highest mammal species richness. Thus, the number of feeding interactions influences the amount of carbon that remains in soils, as animal bodies, feces, and fruits processed by mammals all become sources of soil organic matter. Likewise, in tropical aquatic systems, consumer-mediated nutrient recycling by fish varies greatly with traits such as consumer body size, body stoichiometry, and trophic position. Fish can modulate nutrient cycling in tropical streams (Taylor *et al.* 2006, Capps *et al.* 2013), and fish extinctions can have profound consequences on rates of nitrogen and phosphorus remineralization (McIntyre *et al.* 2007).

Functional diversity can further contribute to community and ecosystem resilience to perturbation, including climate change or defaunation. For example, plant traits such as the ability to withstand water and temperature stress can determine how composition dynamics, plant biomass, and carbon sequestration of Amazonian forests respond to prolonged periods of drought (Levine *et al.* 2016). Models suggest that forests with high plant trait diversity will regenerate more rapidly than forests with low plant trait diversity following the loss of large trees to climate change. Thus, scientists forecasting climate change impacts on Amazonian forest composition, biomass, and carbon sink function over the next century cannot neglect trait diversity (Sakschewski *et al.* 2016). Functional redundancy posits that in biodiversity-rich ecosystems like the Amazon, the extinction of some species will not cause a substantial loss in ecosystem function if remnant species play equivalent roles and are capable of taking over the functions played by extinct species (Lawton and Brown 1993). Indeed, evaluations of seed dispersal networks in Amazonian forests show high connectivity and diet overlap among several species and groups of vertebrates, suggesting high redundancy. However, observations show that fragmented and defaunated forests suffer greatly from trophic cascading effects, suggesting complementarity rather than redundancy in large vertebrates (Bueno *et al.* 2013, Arévalo-Sandi *et al.* 2018).

3.6 Incomplete Knowledge of Biodiversity

Even though the Amazon is one of the largest and most intact forests in the world, it is also one of the least known biologically. Its immense size, diversity, and limited access make the task of documenting its biodiversity extremely challenging. Consequently, there are both spatial and taxonomic biases in the data, sometimes severe (Oliveira *et al.* 2016, Schulman *et al.* 2007, Vale and Jenkins 2012). Looking at species locality data in global databases (Figure 3.7), there is a strong spatial bias towards urban areas, research centers, and major access routes (*e.g.*, roads, rivers). At the same time, some parts of the Basin have few or even no data for any taxa, or at least no data that are digitally accessible.

Looking across taxa, there are also strong biases. Most of the data available are for plants or birds (>80% in GBIF). Groups such as butterflies have far fewer data, and hugely diverse groups like fungi and bacteria are almost entirely unknown. Of course, such taxonomic biases are not unique to the Amazon; they exist for most areas of the world, a consequence of society having more interest in some taxa than others. There are also substantial numbers of still undescribed species, even for well-known taxa (Pimm *et al.* 2010). These species are also unlikely to be like ones already known. Yet-to-be-discovered species are certainly rarer

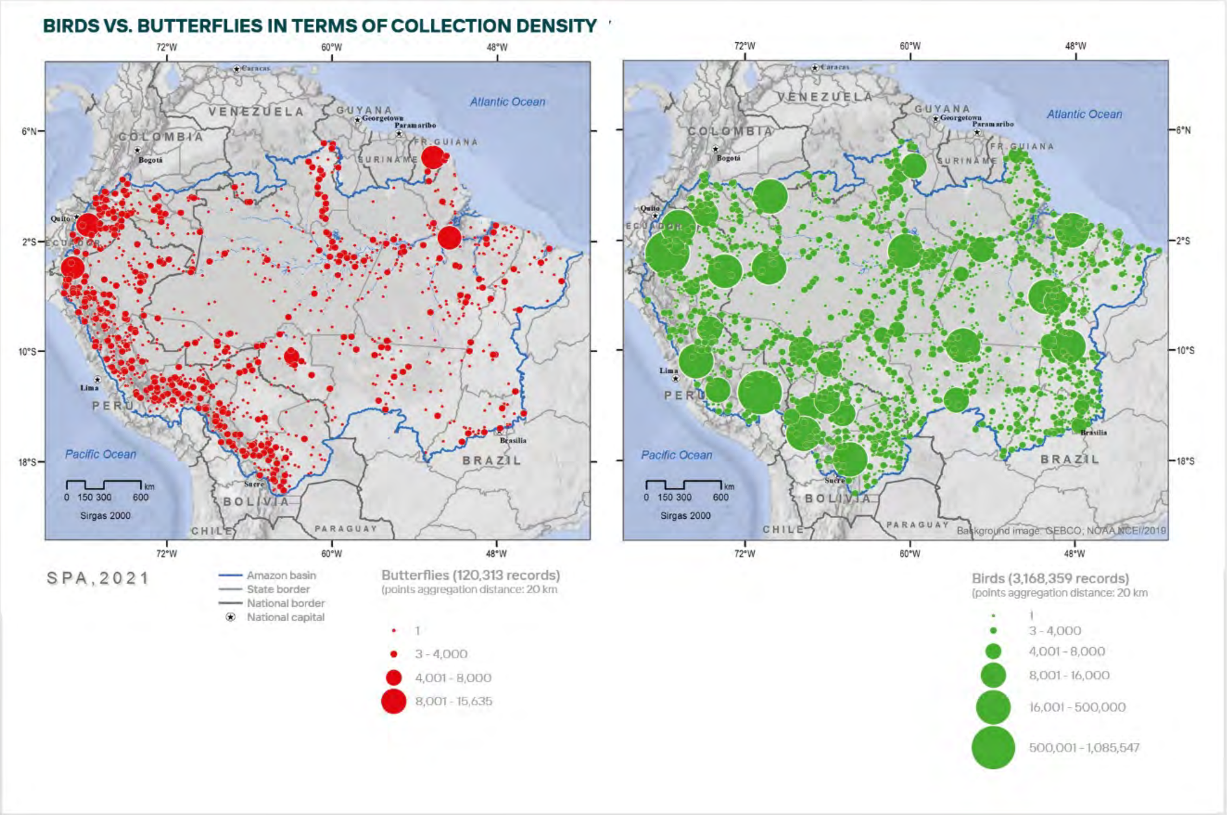


Figure 3.7 Butterflies (120,313 records) versus birds (3,168,359 records) in terms of collection density. Source: GBIF 2021. Data clustering method: Natural Jenks, Aggregation distance: 20 km.

and more restricted in their distributions than already known species. In general, it is the common and widespread species that are described first (Pimm and Jenkins 2019). Consequently, the biodiversity we do not yet know may not follow the same patterns as the biodiversity we do know today.

These spatial and taxonomic biases in the data, and our general lack of adequate data overall, affect our capacity to understand the true patterns of biodiversity in the Amazon. This includes questions such as precisely where centers of endemism are and where one might find the most endangered species, matters of great concern for conservation. Nevertheless, while such limitations in our knowledge are problematic, the reality is that all places have incomplete data. We must make decisions using the best information available, recognizing that as we learn more, it may be wise to improve upon past decisions.

3.7 Conclusions

The Amazon is a global icon of biodiversity. Still, in many taxonomic groups, species diversity is notoriously undescribed, and in-depth taxonomic studies reveal extensive cryptic diversity. As a result, estimating species richness in the region is a challenging task. Biodiversity patterns display considerable variation within the Amazon Basin, with some groups being more diverse in lowland rainforests and others in Andean environments. We are still learning about the fascinating diversity of Amazonian fauna, flora, and fungi, and this knowledge is critical for the conservation of the Amazon region.

Plant-animal and trophic interactions are central ecological processes in Amazonian forests, without which these forests would cease to exist. These networks of mutualists and consumers regulate all aspects of Amazonian forests, and are responsible for their composition, species regulation, recovery from disturbance, and the generation of biodiversity. Changes to species interactions can have cascading effects on Amazonian ecosystem function and the services they provide humanity. An overwhelming and central result from the study of Amazonian forests is that intact plant-animal interaction networks are essential for the resilience of forest biodiversity to anthropogenic change, and for the recovery and restoration of Amazonian systems.

Aquatic ecosystems in the Amazon are a complex mosaic of habitats influenced by flood pulses and by the pattern of nutrient flow. The juxtaposition of low and high productivity waters promotes complex adaptation processes among native organisms. Migratory fish play important ecological roles in Amazonian aquatic food webs, transferring energy and nutrients among different components of the ecosystem, either as predators, prey, engineer species, or seed dispersal agents. Modification or disruption of their migratory patterns by overharvesting, impoundment, or habitat degradation alters ecosystem processes and trophic cascades, primary production, detrital processing, and subsidies transfer over wide spatial scales.

Both inter- and intra-specific variation in functional traits in Amazon biota is enormous. Functional diversity determines species competitive ability and coexistence, diversification, invasion ability, community and ecosystem structure and function, adaptations along environmental gradients, and resistance to disturbance and environmental change. Functional diversity, for example, can further contribute to community and ecosystem resilience to perturbations, including climate change. Therefore, scientists forecasting climate change impacts on Amazonian forest composition, biomass, and carbon sink function over the next century cannot neglect trait diversity.

Existing spatial and taxonomic biases in biodiversity data in the Amazon affect our capacity to understand the true patterns of biodiversity in the region. These gaps include questions such as the location of centers of endemism, areas with the most endangered species, and other questions of great concern for conservation. Although such knowledge gaps may be problematic, they should not prevent decision-making informed by current knowledge and open to incorporating novel information as it becomes available. Public policies are of extreme importance for supporting biodiversity-based basic and applied research in the Amazon, involving transnational and diverse research teams.

3.8 Recommendations

- Promote field-based, laboratory, and collection-based herbarium/museum studies and research collaborations that seek to compile a comprehensive catalog of Amazonian species, complemented with properly preserved vouchers and their tissues/DNA extracts (for molecular studies).
- Support taxonomy, currently an underfunded and underappreciated discipline. We need more taxonomists working alongside molecular biologists and local people willing to contribute their wealth of traditional knowledge towards the description of new species.
- It is crucial to maintain altitudinal connectivity from the Amazon to the Andes. Otherwise, species will lose the ability to migrate in response to climate change.

It is essential to establish large-scale, landscape-level, conservation initiatives that maintain core areas and connectivity to secure the survival of wide-ranging species, migratory species, rare species, species with patchy distributions, and the diversity of functional traits.

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Box 3.2 Trends in the Discovery of New Species of Vertebrates in the Amazon Basin

Each year, new species of vertebrates from the Amazon are described, a process of discovery that began several centuries ago. The first Amazonian vertebrates were described by Linnaeus in 1758: 13 fish, 10 amphibians, 50 reptiles, 131 birds, and 51 mammals. To analyze trends in the descriptions of Amazonian species, 2,406 species of fish were taken as reference (Jézéquel *et al.* 2020), 997 species of amphibians (GBIF: 10.15468/dl.9mgq7k), 804 reptiles (GBIF: 10.15468/dl.uy6mw9), 2,736 birds (GBIF: 10.15468/dl.3zkc3v), and 974 mammals (GBIF: 10.15468/dl.ttgkq4), for a total of 7,827 species (Figure B3.2.1). This exercise does not aim to determine the total number of species in the Amazon, but rather to describe trends in the rate of species descriptions.

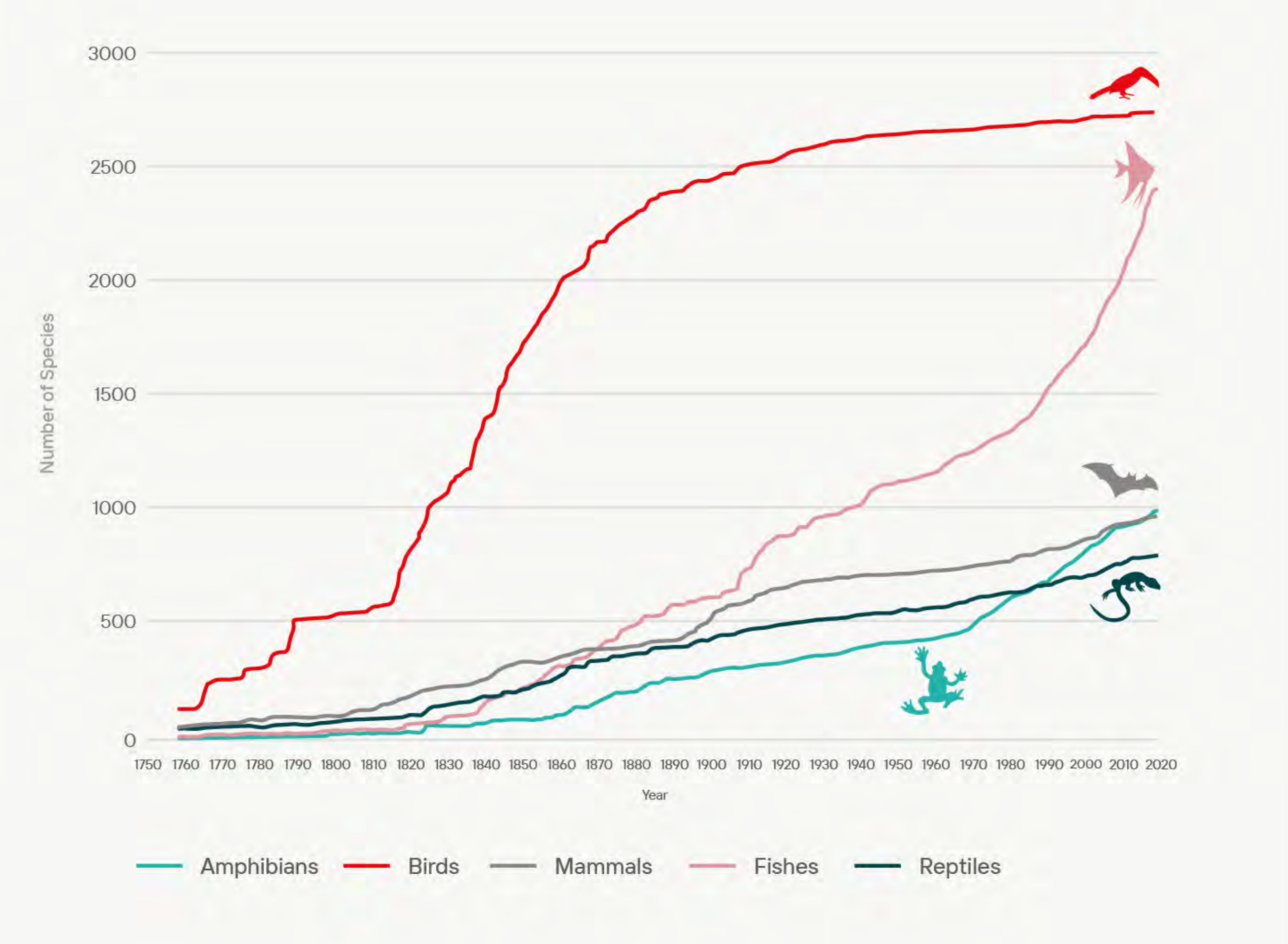

Figure B3.2.1 Species accumulation curves for five vertebrate groups from the Amazon Basin.

Fish After the first species descriptions made by Linnaeus, there was a period with a very low rate of descriptions until 1830. Starting with contributions from naturalists such as Achille Valenciennes (1794–1865) and Johann Jakob Heckel (1790–1857), there was a sustained increase until the beginning of the 20th century. Around 1910, with the main contributions of Franz Steindachner (1834–1919) and Carl H. Eigenmann (1863–1927), there was a significant increase from approximately 600 species to just over 1,000. Between 1940 and 1980 there was a constant increase, but it is remarkable that, since then, when the number of species was at 1,355, there has been a sustained exponential increase in the number described. Indeed, between 2010 and 2020, the largest number (n=412) and proportion (17%) of species were described of any decade (Figure B3.2.2). Between 1980 and 2019, 44.3% of the Amazon species were described.

Since 2016, a rate equivalent to one new species every week has been reached. This is also reflected by the historical peak of descriptions reached in the last decade with a total of 412 species (Figure B3.2.1). According to Jézéquel *et al.* (2019), the Amazon Fish database (https://amazon-fish.com) recognizes 2,406 valid species (Jéjéquel *et al.* 2019), with a clear tendency to continue adding new ones. In time, fish may become the vertebrate group with the highest number of species in the Amazon.

Amphibians The rate of descriptions of new amphibians was very low until 1860, when it increased and remained relatively constant until 1970 (Figure B3.2.3). From the 1970s onward the rate dramatically increased, with 50.65% of Amazonian species described in the last 50 years.

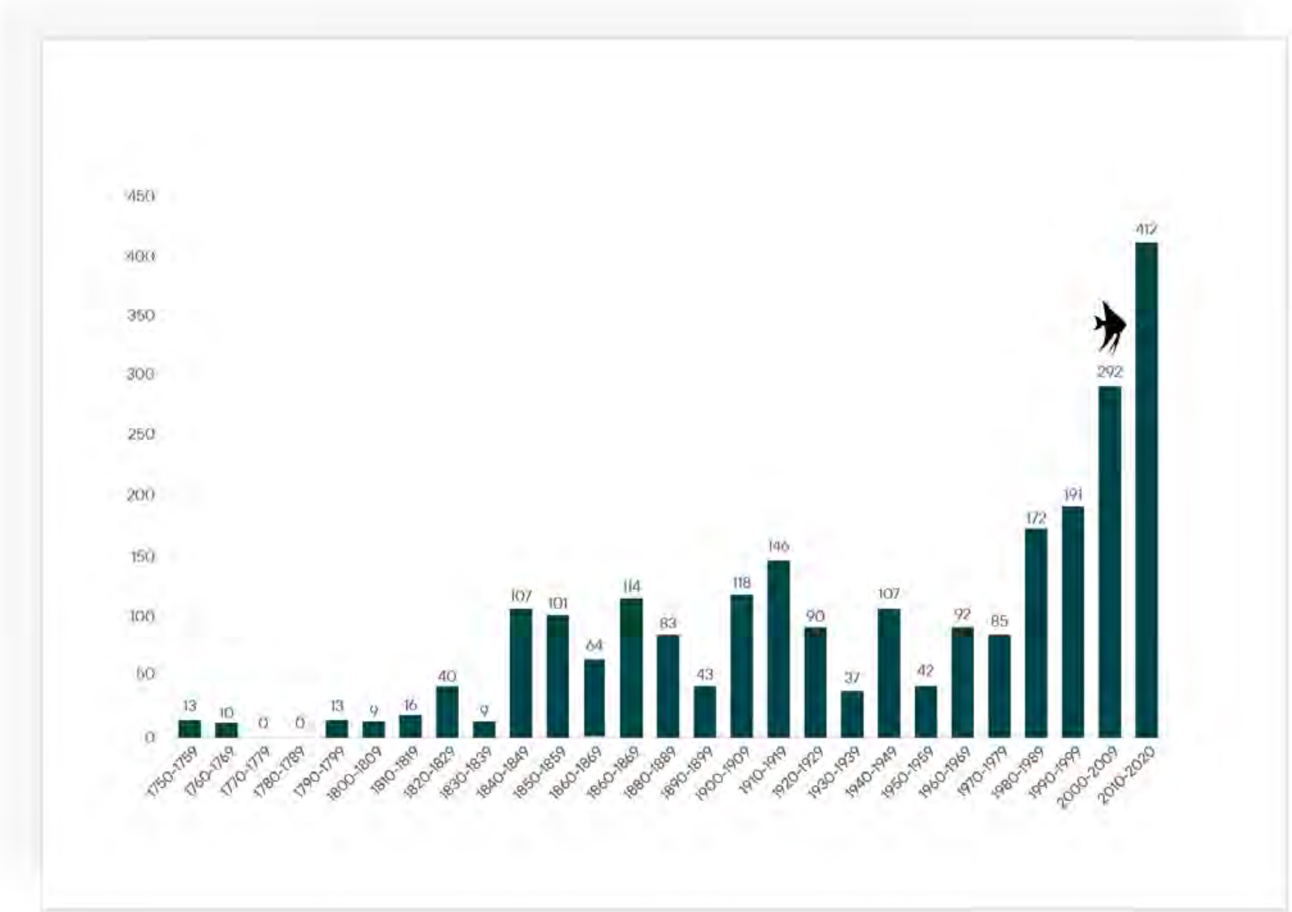

Figure B3.2.2 Number of fish species described per decade in the Amazon Basin

In the 1990s and 2000s, description peaks were reached with 128 and 118 species, respectively (Figure B3.2.3). According to the data available at the GBIF, 997 valid amphibian species have been described for the Amazon, with a tendency to continue increasing, and constituting a priority group of vertebrates for taxonomic efforts. Species discovery has benefited from the incorporation of molecular and acoustic data, as well as the increased number of herpetologists in South America.

Reptiles Since Linnaeus's initial descriptions of 50 species (1758), reptiles are the group of vertebrates with one of the lowest rates of description (Figure B3.2.1), and the lowest number of species described to date (804). Although descriptions have continuously increased, there is not a period of marked increase as with other vertebrate groups, perhaps highlighting the need for further taxonomic efforts. In the 1860s, a peak of descriptions was reached with 74 species (9%), whereas in recent decades, between 1990 and 2010, there was an increase in the number of species described, reaching a peak of 54 between 2000 and 2009 (Figure B3.2.4).

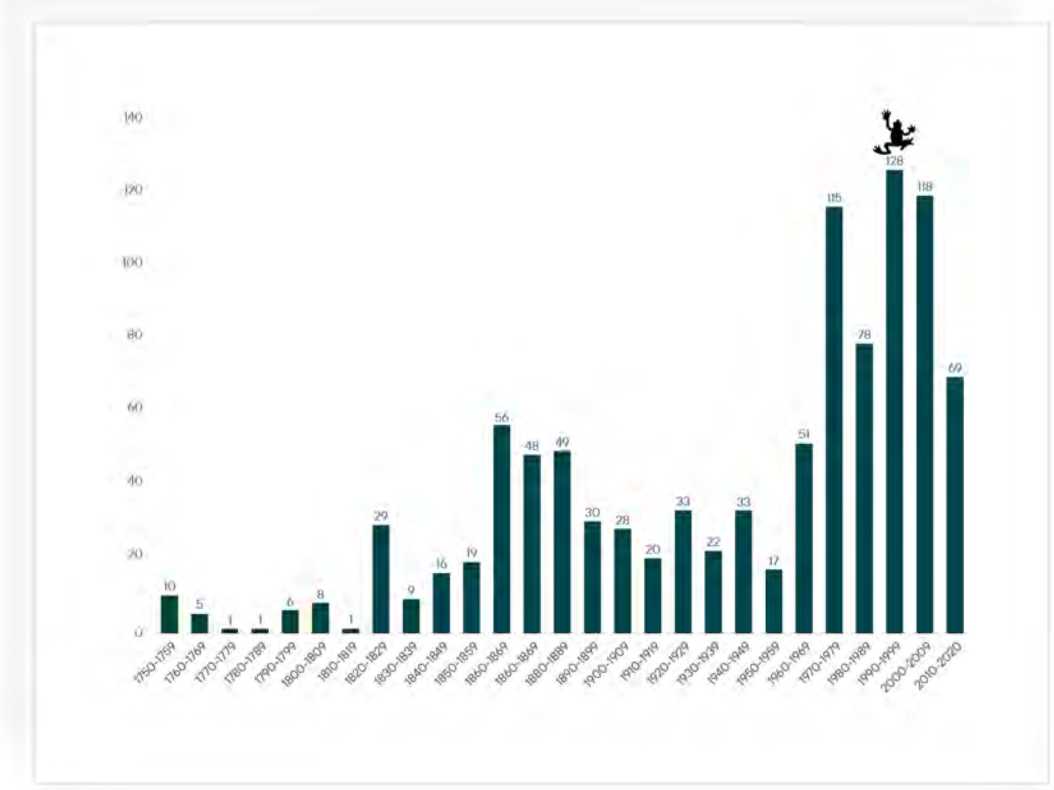

Figure B3.2.3 Number and percentage of amphibian species described by decade in the Amazon.

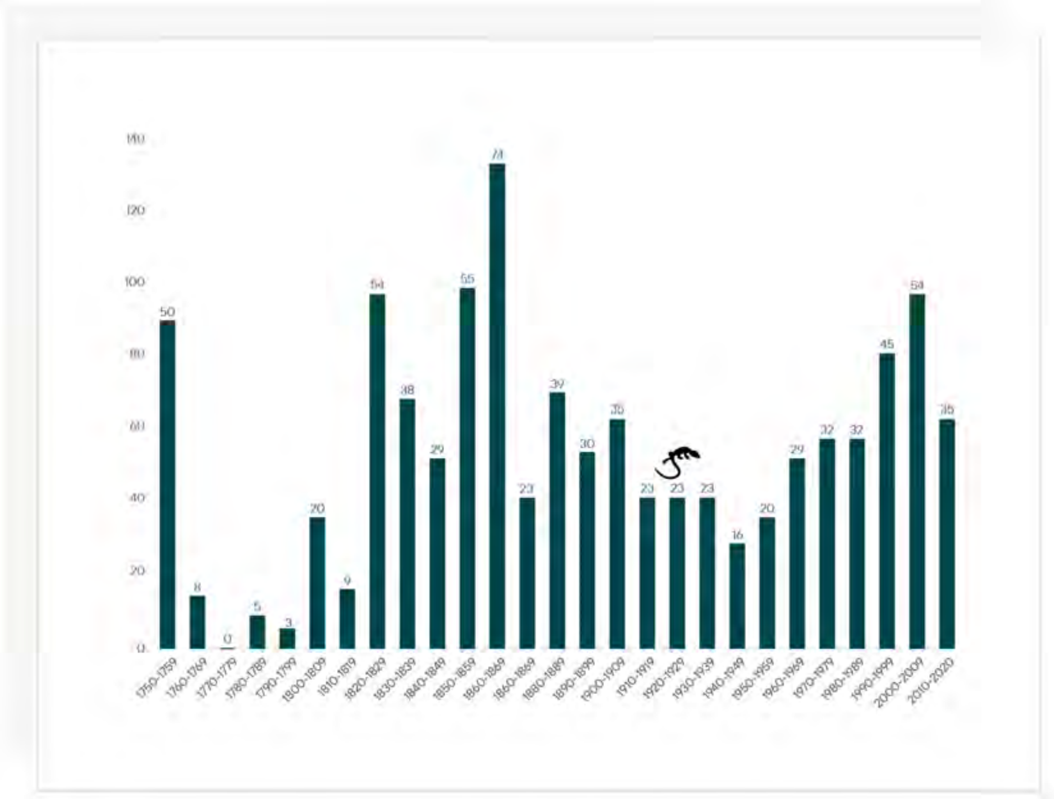

Figure B3.2.4 Number and percentage of reptile species described by decade in the Amazon.

Birds Since Linnaeus described 150 bird species, this is the vertebrate group with the largest number of species, currently with 2,736 according to GBIF data (Figure B3.2.1). Although there was very little increase between 1790 and 1810, the number of species rapidly increased to 2,500 by 1910. The peak of Amazon species descriptions occurred between 1840 and 1849, with 349 species added (17%), accounting for 58.2% of species added between 1810 and 1870 (Figure B3.2.5). Since 1910, species descriptions have significantly slowed down, with just 25 species added since the turn of the century. This trend suggests that birds are the best-known vertebrate group with the least number of species remaining to be described.

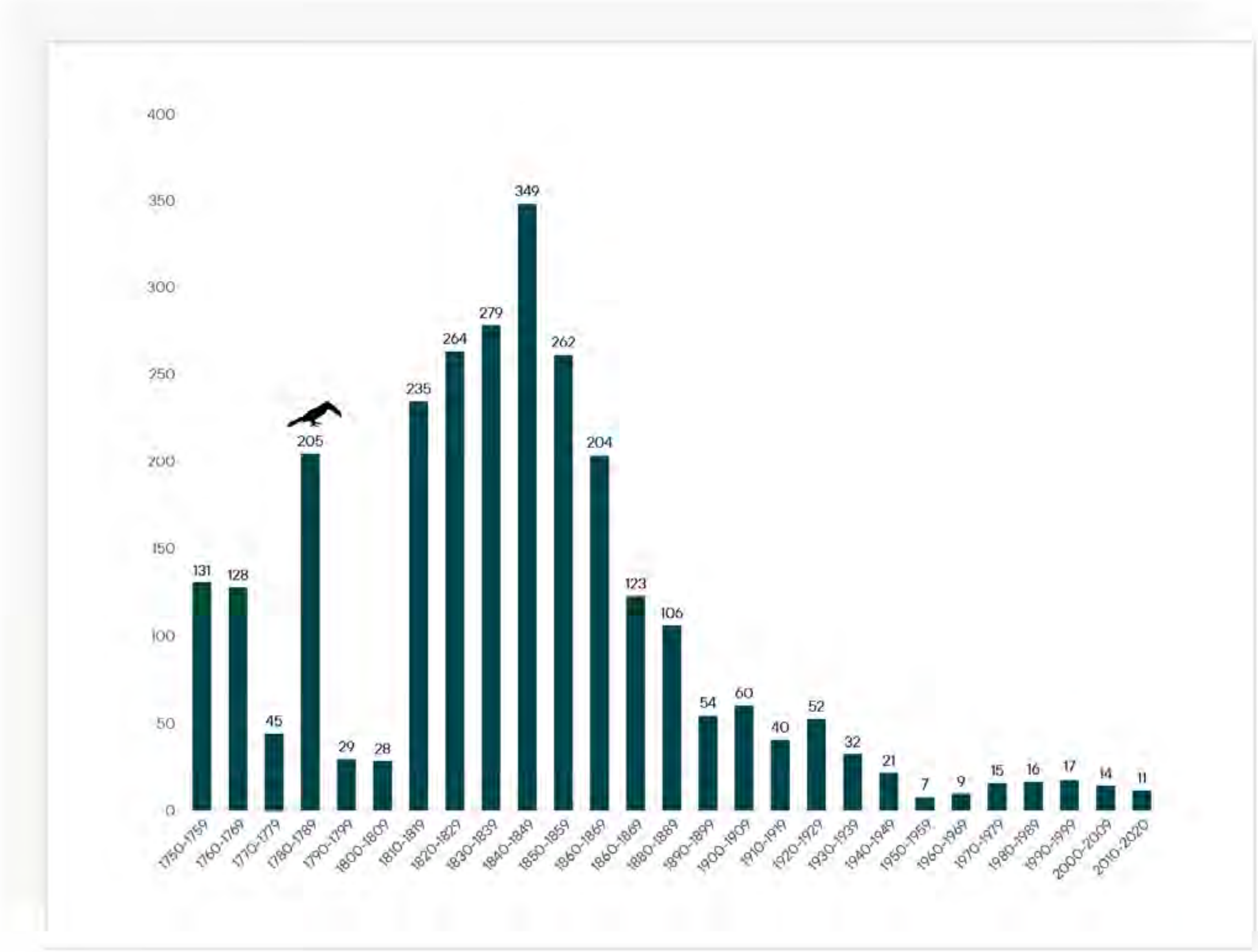

Figure B3.2.5 Number and percentage of bird species described by decade in the Amazon.

Mammals When descriptions of Amazonian mammal species began (51 species described by Linnaeus in 1758), they occupied second place, after birds (Figure B3.2.1). The number of mammal species moved to third place between 1860 and 1870, a position it held until the last decade, when amphibians overtook mammals (975 vs 997, respectively) (Figure B3.1 and Figure B3.2.6).

The rate of descriptions has remained relatively constant with increases in 1840 and 1900–1920, with the latter period being the peak in descriptions (92 species, 9%, Figure B3.2.6). The greatest potential for further new mammal species in the Amazon are among bats, rodents, and marsupials.

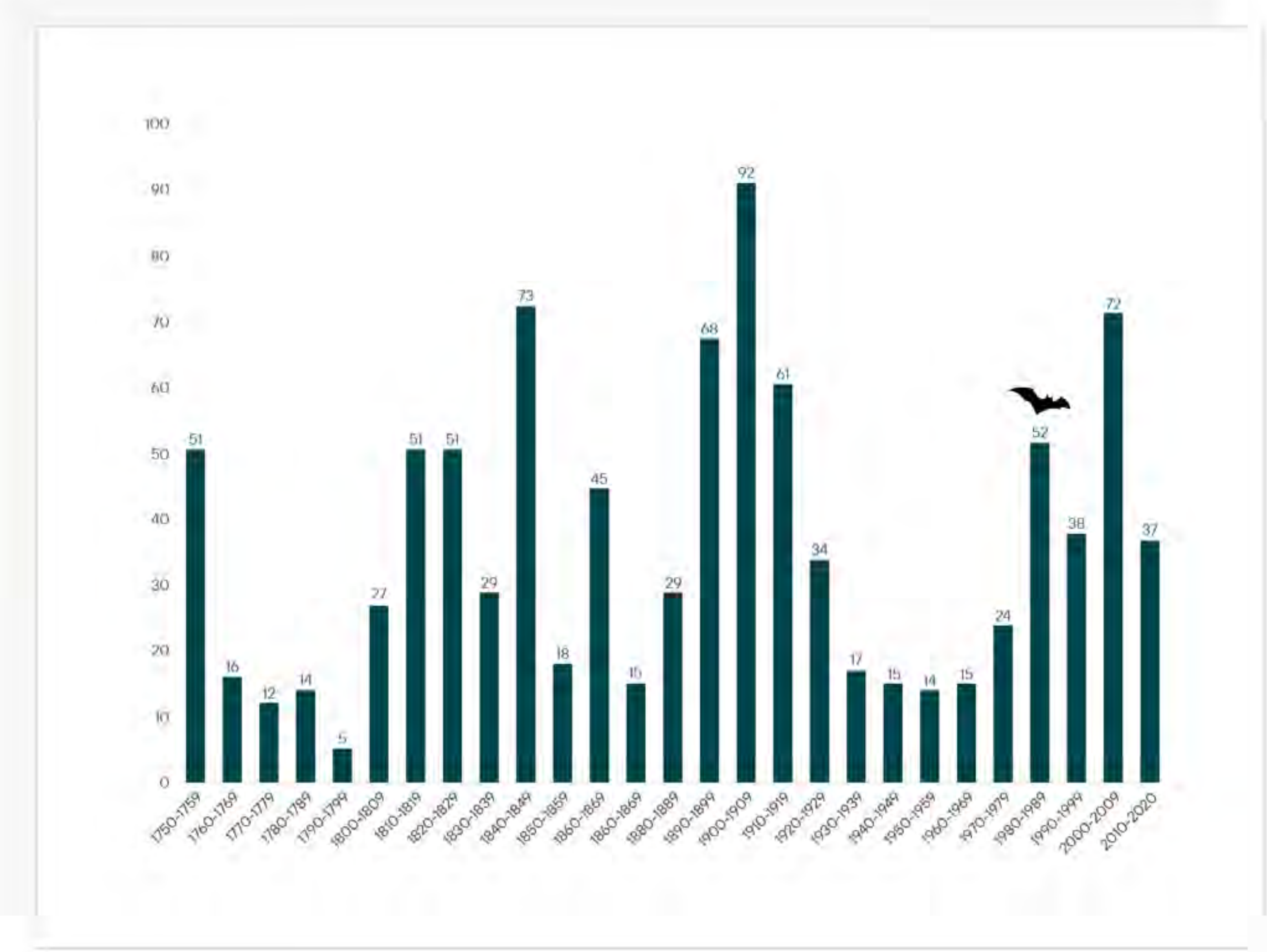

Figure B3.2.6 Number and percentage of mammal species described by decade in the Amazon.

Patterns of discovery vary widely among vertebrate classes in the Amazon, and the rates of new species descriptions, for each decade, have been highly variable between groups. To continue with the high rates of new species descriptions, particular attention should be given to the formation of integrative taxonomists, especially for fish, amphibians, and small mammals, whose species accumulation curves are far from reaching an asymptote, as happens in birds. New species are being continually described in the Amazon, including areas affected by the negative impacts of human activities. Efforts to describe new species before they are lost to habitat destruction must be intensified if we want to know the true levels of species richness in the Amazon, and the most effective ways to preserve it.

Methodological note: Species lists with the year of description for each species were used in the analysis. In the case of fish, the list available from Amazon Fish (Jézéquel *et al.* 2020) was used, while for the rest of the groups the species lists were extracted from the GBIF, using a polygon that covers the entire Amazon basin (Amphibians, DOI: 10.15468/dl.9mgq7k; reptiles, DOI: 10.15468/dl.uy6mw9; birds, DOI: 10.15468/dl.3zkc3v; and mammals, DOI: 10.15468/dl.ttgkq4). In all cases, it is assumed that GBIF and Amazon fish lists have the taxonomic information reviewed and validated. Only the scientific names that include author and year were used, so the species totals do not necessarily indicate the total number of species present in the Amazon. The polygon drawn for the GBIF download may have omitted some species or included species that do not necessarily occur in the Amazon.

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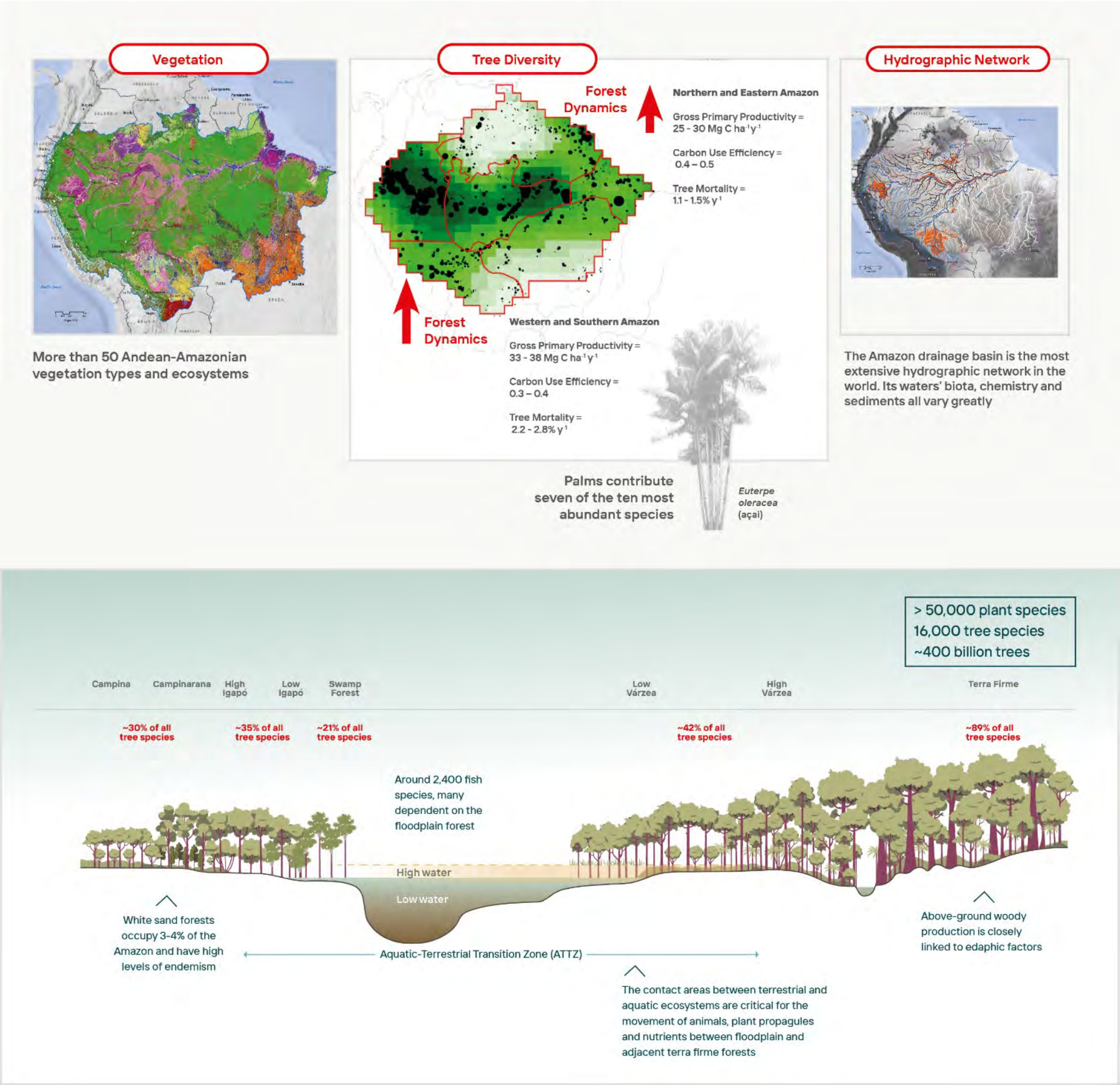
Chapter 4

Amazonian ecosystems and their ecological functions

Cipó parasita estrangula árvore (Foto: Leonardo Milano/Amazônia Real)

INDEX

Graphical Abstract



More than 50 Andean-Amazonian vegetation types and ecosystems

Palms contribute seven of the ten most abundant species

The Amazon drainage basin is the most extensive hydrographic network in the world. Its waters' biota, chemistry and sediments all vary greatly

Around 2,400 fish species, many dependent on the floodplain forest

White sand forests occupy 3-4% of the Amazon and have high levels of endemism

The contact areas between terrestrial and aquatic ecosystems are critical for the movement of animals, plant propagules and nutrients between floodplain and adjacent terra firme forests

Above-ground woody production is closely linked to edaphic factors

Figure 4A Graphical Abstract

Biodiversity and Ecological Functioning in the Amazon

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Key Messages

- Between the Andean mountains and the Amazon plain, a diverse mosaic of ecosystems and vegetation is represented by forest, savanna, and swamp biomes. The key to understanding the ecology of the Amazon region is to integrate functional processes between terrestrial and aquatic components, across multiple biophysical gradients, from the continental divide to the ocean.
- Amazonian lowland forests, covering 5.79 M km^2, is likely the richest forest area globally, holding an estimated 16,000 tree species and perhaps over 50,000 plant species, many of which are still unknown. With close to 400 billion trees, the Amazon is home to 13% of all trees worldwide.
- Species composition is not evenly distributed across the basin but is determined by soil geology and climate. The most diverse forests are found in the western Amazon; however, protected areas are required across the basin for comprehensive conservation. Forests in the western Amazon cover relatively fertile soil, are species-rich, have high stem turnover, and have somewhat lower above-ground biomass. Forests in the central and eastern Amazon, mainly found on poor soils, are less dynamic and have high biomass.
- The Amazon River Basin holds the largest tropical wetland area on Earth, and a vast number of rivers, comprising not only the world's largest store of freshwater, but also 15% of all fish species.
- Forest composition is already being affected by climate change, with the mortality of wet-soil affiliated genera having increased in places where the dry season has strengthened the most. Given climate change projections for this century, such changes are likely to intensify.
- Amazonian ecosystems result from a mixture of terrestrial and aquatic landscapes in often extensive floodplains, whose dynamics are affected by the tectonic uplift of the eastern Andean slopes and the much less geologically active lowland Amazon River Basin. The contact areas, or ecotones, between terrestrial and aquatic ecosystems (fresh and marine waters) are of critical importance for the dynamics of the whole region. They contribute to the movement of animals, plant propagules, and nutrients between the floodplain and adjacent *terra firme* forests, and promote habitat heterogeneity.

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- Because of its size and the carbon density of its ecosystems, the Amazon forest is a huge carbon store. Spatial variation in Amazonian biomass, carbon stocks, and biomass dynamics is driven more by soil conditions than climate and more by spatial variation in tree mortality than productivity.
- Amazonian wetlands also store large amounts of carbon due to the extensive and deep accumulation of below-ground peat deposits (e.g., >3 Pg C in north-western Amazonian swamps). Hence, their conservation also plays a crucial role in modulating global warming.

Abstract

Amazonian lowland tropical rainforests cover ~5.79 million km^2. Based on geology, the Amazon lowland forest area can be divided into six regions. The Guiana Shield and Brazilian Shield (in the southern Amazon) are on very old, nutrient-poor soils, while the Western Amazonian regions (northern and southern) and the regions along the Amazon River are mainly built from more recent sediments of Andean origin and of variable nutrient richness. The six regions are characterized by differences in soil fertility and rainfall, causing differences in above-ground biomass, productivity, and tree turnover. There is still intense debate concerning the total plant species richness of the the Amazon. A well-supported estimate for trees (diameter >10 cm) is 16,000 species, ~11,000 of which have been collected and described. Estimates of the total flora range from 15,000 to 55,000 species. As in much of the tropics, Fabaceae (the bean family) are the most species-rich of the major woody groups in the Amazon. South America and the Amazon are also renowned for the abundance and diversity of palms. While most ecosystem vegetation models emphasize climate and carbon production processes, these are not sufficient to understand how Amazonian forest ecosystems vary spatially. In particular, long-term observations with plots show that spatial variation in Amazonian forest biomass and stem dynamics are driven more by soil conditions than climate, while carbon stocks are constrained as much by soil physical features and tree floristic composition as by productivity. The key effects of soil on the Amazon's ecosystem function also extend to animals and their important functions, including herbivory, seed dispersal, and insect activity. Soil and geology influence Amazonian rivers too, which are distinguished as being either white-water (carrying sediments from the Andes), clear-water (draining the ancient Shields), or black-water (draining white sand areas). The nutrients associated with each major river class strongly determine the floodplain forest ecology and species, with *igapó* in sediment-poor clear and black-waters, and *várzea* (known as *tahuampa* in Peru) with white, sediment-rich waters. Climate impacts become stronger towards the margins, and some Amazon forests are already close to the thermal and hydrological limits of sustaining productive forest ecosystems. Amazonian tree mortality rates are already increasing in many intact forests, Amazonian forest composition has been affected by recent droughts, and the mortality of wet-affiliated Amazonian tree genera has increased in places where the dry season has intensified. Key areas of uncertainty include understanding the extent to which recent climate change has caused a slowing of the carbon sink in intact Amazonian forests, and whether intact forests will now lose carbon, or whether the shallow water tables and rich biodiversity of many Amazonian forests will buffer against climate change, especially in the western part of the basin.

Keywords: Amazonian ecosystems, aquatic ecosystems, forest dynamics, ecological features, ecosystem processes, interactions, river systems, terrestrial ecosystems.

4.1. Amazonian Ecosystems: An Introduction

The Amazonian biogeographical region, including the lowland Amazon and Orinoco River Basins and adjacent upland areas of the Guiana and Brazilian Shields, covers about 8.4 million km^2 of northern South America (see Chapter 2). The Amazon River basin (7.3 million km^2), including the Tocantins and Araguaia Basins, covers 41% of South America, encompassing two of the major South America biomes, tropical moist forests and tropical savannas (Coe *et al.* 2008). The Amazon region is considered one of the most important ecological regions in the world, because it includes the largest area of continuous tropical moist forests, estimated to cover 5.79 million km^2 (Ter Steege *et al.* 2015) and an estimated >10% of all known species of vertebrates and vascular plants on Earth are estimated to live there (Chapter 2). It also contains by far the largest tropical floodplain system (Keddy *et al.* 2009), constituted by a rich mosaic of terrestrial, aquatic, and transitional ecosystems subjected to seasonal or permanent waterlogging (Salo *et al.* 1986) (Figure 4. 1).

The ability of ecosystems to capture, process, and store carbon and other nutrients is determined by key climatic, edaphic, and biological factors. The Amazon, with the largest tropical rainforest on the planet, encompasses significant differences in precipitation regimes but even greater differences in the geological origin, age, and nutrient richness of the soils that support its ecosystems (see Chapter 1). Here we review the role of these factors in controlling forest composition and processes, especially those related to productivity and forest dynamics. For example, Amazonian forest biological, structural, and functional diversity is fundamentally affected by water and nutrients. Hydrology defines their higher-level classification as *terra firme* forests, seasonally flooded forests (várzea, igapó), and swamp forests. Freshwater ecosystems cover more than 1 million km^2, consisting of three main water types: white, black, and clear waters, which differ in their origin and sediment composition. Within the extensive non-flooded forests, distinctive and extremely poor white sand forests may be found, especially in the upper Rio Negro area and the Guianas (see Adeney *et al.* 2016).

In this chapter we summarize information on Amazonian ecosystems and their ecological functions, with a primary focus on trees. We start with a short description of the vegetation types of the Andes, followed by a more detailed description of the lowland Amazonian terrestrial vegetation types, and conclude with the vast wetlands included in the area. We continue with an analysis of the main ecosystem functions (e.g., terrestrial and aquatic), with an emphasis on productivity and carbon sequestration. The aim of this chapter is to reveal the enormous variation of vegetation types, their diversity and functioning, and how this is affected by soil, climate, and flooding dynamics.

4.1.1. Vegetation types from the High Andes to the Atlantic Ocean

Alexander von Humboldt's *Tableau Physique* (Humboldt 1805) is, arguably, the first published overview of plant composition in northern South America as a region (Figure 4.2). His travels extended from the Pacific to the Atlantic Oceans and passed Chimborazo, the highest equatorial volcano in Ecuador (Ulloa Ulloa and Jørgensen 2018).

Humboldt depicted the biotic and physical characteristics, and changes in vegetation structure and composition along an elevation gradient, from the tree-dominated lowlands to the treeless páramo bordering the snow line.

Plant communities in the high Andes (above 3,000 m) are known as 'páramo' in the more humid areas of the northern Andes of Venezuela, Colombia, and Ecuador, and 'jalca' in northern Peru (Madriñán *et al.* 2013); 'puna' is found in the southern, drier Altiplano of Peru and Bolivia (Sánchez-Vega and Dillon 2006).

Páramos and punas are grass-dominated ecosystems with plants uniquely adapted to these extreme environments of cold temperatures, low pressure, and extreme solar radiation, with prominent rosette forming plants, such as those in the genera *Espeletia* and *Puya.* Only a few species of trees, such as those in the genera *Buddleja, Gynoxys*, and *Polylepis,* reach the highest elevations, up to 4,700 m (Hoch and Körner 2005).

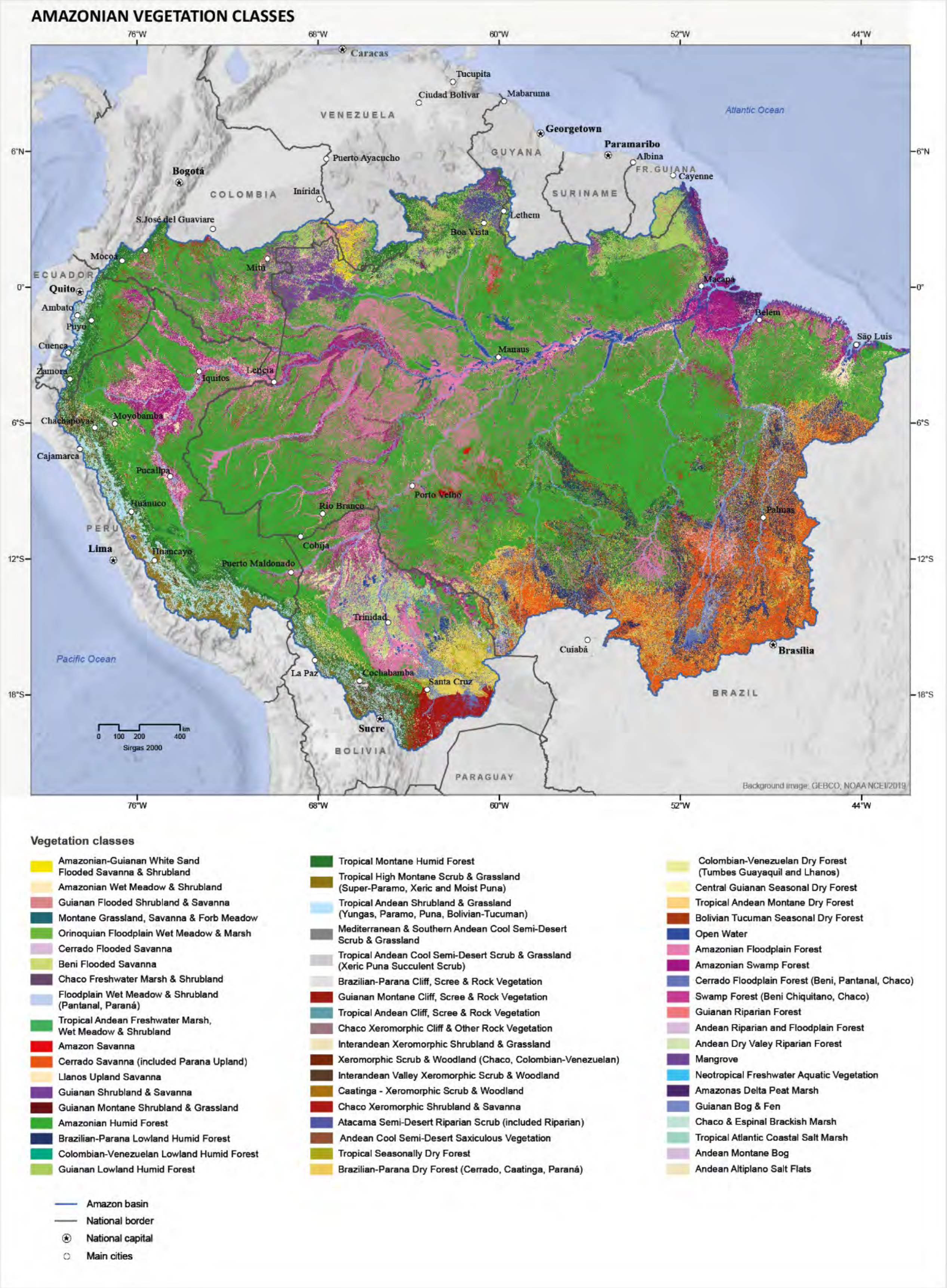


Figure 4.1 Map of Amazonian vegetation and ecosystems (Source: Comer *et al.* 2020). The solid gray box highlights the high richness of vegetation and ecosystems found in the latitudinal and altitudinal gradients in the Amazon (see Figure 4.4 for detail).

Upper montane forests traverse humid sites from 2,500 to 3,900 m elevation. Montane forests are among the most species rich vegetation types to be found in the tropical high Andes (Gentry 1988). These forests are 5 to 20 m tall with emergent trees reaching 35 m or more, but with smaller individuals at the treeline, in places where soils are shallow, or where disturbances altered past vegetation. Lower-Montane forests are found at middle elevations, between 1,000 and 2,500 m, and can be as diverse and complex as forests found in humid tropical lowlands. Intermontane valleys cut through the tropical Andes, reaching as low as 2,000 m. Andean and Amazonian species and ecosystems form spatial mosaics in the alluvial valleys above 1,000 m, surrounded by slopes covered by montane forests (Josse *et al.* 2009). Below 1,000 m, Andean submontane forests gradually change into Amazonian lowland forests, defined here as those below 500 m, which cover most of the basin. Overall, the Andes mountains are extraordinarily diverse due to their climatic and topographic complexity, their size, and their position spanning the Equator, northern, and southern tropical zones. Including the forests of the eastern flanks of the Andes, which merge into the Amazonian lowlands, they have exceptional levels of diversity and endemism, combined with ongoing rapid deforestation and land use changes (e.g., Young *et al.* 2007).

4.2. Lowland Amazonian Ecosystems

4.2.1 Terrestrial Ecosystems

Figure 4.2 Alexander von Humboldt's *Tableau Physique* (Humboldt 1805), a graphic overview of plant communities, from the Pacific to the Atlantic Ocean and passing over the Andean mountains. Reproduced with permission from the Peter H. Raven Library at the Missouri Botanical Garden (https://www.biodiversitylibrary.org/page/9869921).

4.2.1.1 Lowland Rainforests

Amazonian lowland rainforests cover approximately 5.79 million km^2 over nine countries (ter Steege *et al.* 2013, ter Steege *et al.* 2015). Mean annual rainfall varies from especially humid forests in the northwestern Amazon (over 3,000 mm) to drier, more seasonal systems in the south (1,500 mm) (Espinoza-Villar *et al.* 2009). Based on the maximum geological age of the soil producing materials, the area has been divided into six regions (Quesada *et al.* 2011, ter Steege *et al.* 2013). These regions and their tree diversity are displayed in Figure 4.3.

Soils in the northwestern and southwestern Amazon (parts of Colombia, Ecuador, Peru, and also extending into western Brazil and parts of Bolivia), originate from recent (Holocene and Quaternary) Andean riverine sediments or Tertiary estuarine deposits. These are typically more nutrient-rich than the much older clays of the eastern Amazon, and soils derived from the ancient Precambrian Guiana and Brazilian Shields (Quesada *et al.* 2010, 2011). However, the western soils are often less physically favorable to trees, being often shallower, with poorer structure and more prone to water-logging. Overall, therefore, a rainfall gradient runs from the northwest (wet) to the south and southeast (drier), while a more complex soil gradient runs almost orthogonal to this, from the west and south-west (more fertile) to the east and northeast (less fertile). As a result, the lowland forests of the southwestern Amazon have hot, moist, and somewhat seasonal climates very similar to the distant forests of the Guianas, yet soils which are more fertile and, in terms of physical structure and rooting depth, often much less favorable. In spite of the similar climates, there is almost complete turnover of dominant tree species (ter Steege *et al.* 2006). Overlaid on these large-scale basin-wide patterns are complex regional-scale and landscape-scale geomorphological, fluvial, edaphic, and hydrological variations which help create the great biological richness and diversity of Amazonian ecosystems.

The Amazonian forest holds approximately 392 billion individual trees with a diameter of over 10 cm (dbh) (ter Steege *et al.* 2013), amounting to 13% of all trees on earth (Crowther *et al.* 2015). If trees over 2.5 cm dbh are chosen (Draper *et al.* 2021) the number of 392 billion may easily double. The average density is approximately 570 individual trees per hectare, with the highest densities in the wettest parts, notably the northwestern Amazon (ter Steege *et al.* 2003).

The composition of Amazonian forests is determined primarily by soil fertility (ter Steege *et al.* 2006, Tuomisto *et al.* 2019, Chapter 1), and annual rainfall (ter Steege *et al.* 2006, Esquivel Muelbert *et al.* 2016). At the southern climatic margins of the Amazon the forest gradually changes into cerrado (a tree savanna).

Cardoso *et al.* (2017) recorded 14,003 species, 1,788 genera, and 188 families of seed plants in Amazonian lowland rain forest, with one-half of these trees capable of reaching ≥10 cm dbh (6,727 species, 48% of the total flora; 803 genera, 45% of the total genera). More than one-half of seed plant species diversity in the Amazonian rain forests comprises shrubs, small trees, lianas, vines, and herbs (7,276 species, 52% of total flora). Three of these top 10 families are exclusively herbaceous (Araceae, Orchidaceae, and Poaceae, except for bamboos such as *Guadua* species). Although a large proportion of its whole diversity is still not known, ter Steege *et al.* (2013, 2020) estimated that the Amazon may hold close to 16,000 tree species alone – from an estimated total flora that ranges from 15,000 to 50,000 species – of which 10,000 tree species have been collected in the area (ter Steege *et al.* 2016, 2019b). Truly core Amazonian species may be less than this, as many species from the cerrado or higher elevations in the Andes are found in the edges of the Amazon, which may largely explain the difference with the estimate of Cardoso *et al.* (ter Steege *et al.* 2020). Regardless of the true total, Amazonian forests, especially in the western Amazon, include many of the most tree-species-rich ecosystems in the world (Sullivan *et al.* 2017).

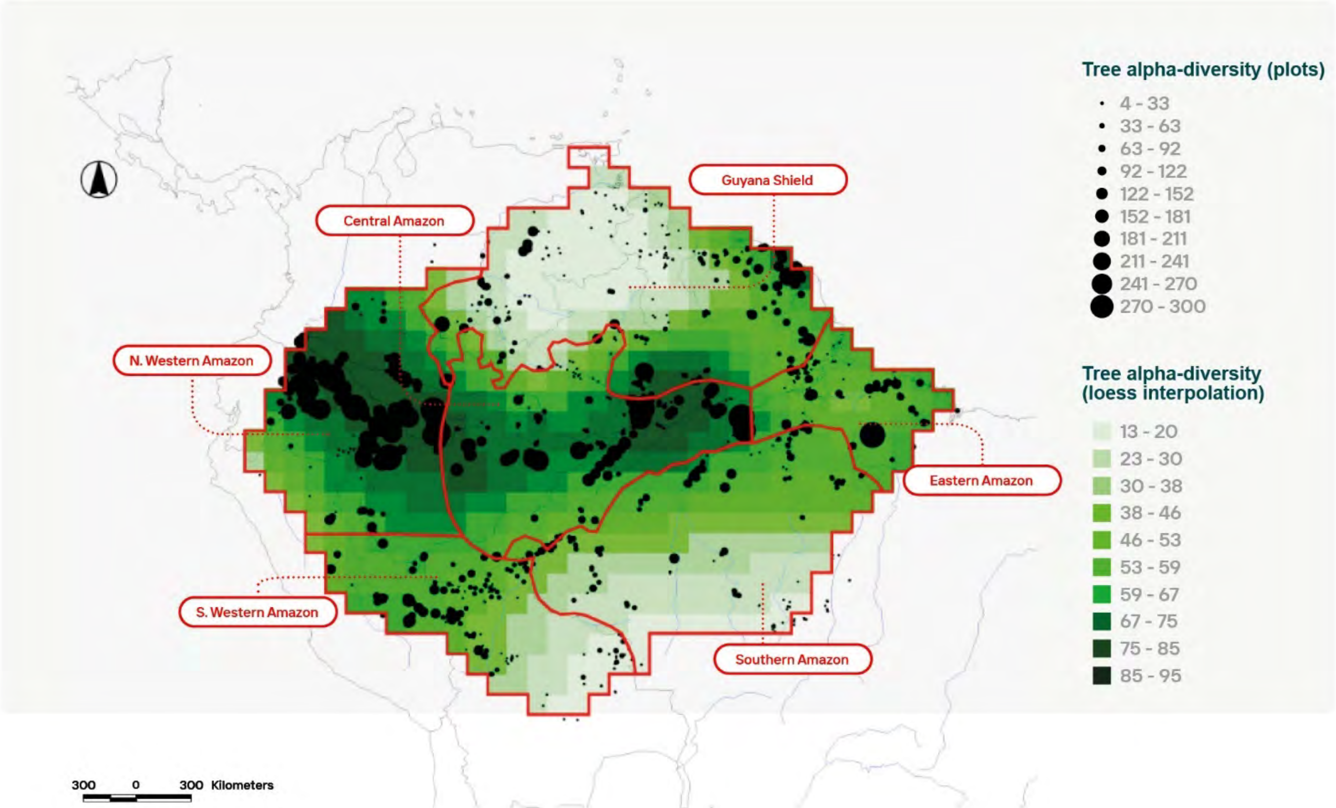


Figure 4.3 Map of tree α-diversity of the Amazon (http://atdn.myspecies.info), based on an interpolation of Fisher's α of 2,282 plots of mostly 1-ha. Black dots: Fisher's α of individual plots. Green background color: the interpolated values calculated for 565 Amazonian 1-degree grid cells (~111 km). In gray the six regions of the Amazon as used in this chapter (Quesada et al. 2011, ter Steege et al. 2013).

More generally, even with a large proportion of its diversity still not described, the Amazon houses a remarkable share of currently documented global biodiversity, holding at least 18% of vascular plant species, 14% of birds, 9% of mammals, and 8% of amphibians found in the Tropics. As one example of the level of mammalian diversity, of the 18 New World primate genera, 14 occur in Amazon, and eight are endemic to the region (da Silva *et al.* 2005).

While the forests are exceptionally diverse, the tree communities at large scale are dominated by relatively few species, and several of these dominants are widespread. As a result, a little over 200 tree species (out of the estimated 16,000) account for half of all trees over 10 cm dbh (ter Steege *et al.* 2013, ter Steege *et al.* 2020).

From mathematical models it can be estimated that over 10,000 species number less than 1 million individuals, while over 5,000 number less than 5,000 individuals. The Amazon thus combines hyper-diversity with hyper-dominance and hyper-rarity.

Ten families contribute 65% of all trees in the Amazon; Fabaceae (47 billion), Arecaceae (26 billion), and Lecythidaceae (20 billion) are the most abundant. The ten most abundant species are *Eschweilera coriacea* (4.7 billion), *Euterpe precatoria* (3.9 billion), *Oenocarpus bataua* (2.8 billion), *Pseudolmedia laevis* (2.8 billion), *Protium altissimum* (2.8 billion), *Iriartea deltoidea* (2.6 billion), *Mauritia flexuosa* (1.9 billion), *Socratea exorrhiza* (1.9 billion), *Astrocaryum murumuru* (1.8 billion), and *Pentaclethra macroloba* (1.7 billion) (ter Steege *et al.* 2020). It is interesting to note that palms

(Arecaceae) are the second most abundant family and contribute seven of the ten most abundant species, yet consist of very few species compared to the most abundant family, Fabaceae. The latter have 789 species in the plot data of ter Steege *et al.* (2020), while Arecaceae have only 74. In fact, Arecaceae are five times more likely to be among the ~220 hyperdominants than would be expected on the basis of its species richness. Fabaceae are also the family with the highest tree species richness in the Amazon with 1,386 collected species (ter Steege *et al.* 2019b), For all seed plants the majority of the species-rich families are small statured or herbaceous, except Fabaceae (Cardoso *et al.* 2017).

Tree species diversity is not evenly distributed across the Amazon (Figure 4.3). The highest diversity is found in the northwestern Amazon and central Amazon where single plots of one hectare may have over 300 tree species (Amaral *et al.* 2000, Gentry 1988). Much lower diversity is the Brazilian and Guiana shields, especially towards the edges of the Amazonian forest.

Species richness is highest in Dryland (*terra firme*) forests (Figure 4.4), especially those of the more fertile western Amazon, and lowest in flooded forests (*várzea*, *igapó*), swamp forests, and white sands. Although fertility and flooding may affect species richness, tree diversity (and its inverse – dominance) is also linked to the total area a particular system makes up in the Amazon (ter Steege *et al.* 2000, ter Steege *et al.* 2019a).

4.2.1.2 White sand forests

White sand forests (known by common names like campinarana, Amazonian caatinga, varillar) are found on pockets of highly leached deposits of podzolized white-sand (Adeney *et al.* 2016).

White sand forests occupy roughly 3-5% of the Amazon, with major occurrence in the upper Rio Negro area and the Guianas (Adeney *et al.* 2016). They are generally species poor, especially in the Guianas, a feature often attributed to their nutrient poorness but more likely a consequence of their small, fragmented area (ter Steege *et al.* 2000, 2019a). Because of the stark soil differences between white sand forests and *terra firme* forests, white sand forests are characterized by high levels of endemism (Adeney *et al.* 2016).

Tree genera typically found in white sand forests include *Eperua, Micrandra, Clathrotropis, Dicymbe, Hevea, Aspidosperma, Protium, Licania, Pouteria, Swartzia* (ter Steege *et al.* 2013). Impoverished areas (often due to burning) tend to have more scrub-like vegetation (locally called campina, bana, muri scrub), often dominated by *Humiria balsamifera,* and in the Guianas by *Dimorphandra conjugata* as well (Lindeman and Molenaar 1959). Because of their isolation in small patches, white sand forests may never recover species that have been lost (Álvarez Alonso *et al.* 2013). White-sand ecosystems in the central Amazon still remain inaccessible and poorly studied (Adeney *et al.* 2016).

4.2.1.3. Savannas and grasslands

Savanna vegetation is characterized by the presence of up to 40% tree cover, often less than 8 m tall, with a graminoid layer. Savanna occupies 14% of the Amazon basin (including the Tocantins-Araguaia basin) and is distributed in *terra firme* in the southeast of the Brazilian Amazon, and in permanently or seasonally flooded sites, as in Beni savanna in Bolivia, in patches of open savanna under washed white sand across the Amazon, or on degraded lands subject to fire. White sand savannas are mainly found in the upper Rio Negro area and the Guianas (see above). Savannas extend over sandy-clay substrates and eventually form forest islands – around 0.3 to 1.5 km^2 – mixed with swamps in depressions and gallery forests within the basin, which are part of the drainage system of the whole landscape. Woody savannas on *terra firme* or slighty higher-relief terraces of the alluvial plain are formations with species of *Curatella americana, Anacardium microcarpum, Hancornia speciosa, Qualea grandiflora, Byrsonima crassifolia,* and *Tabebuia* spp., as

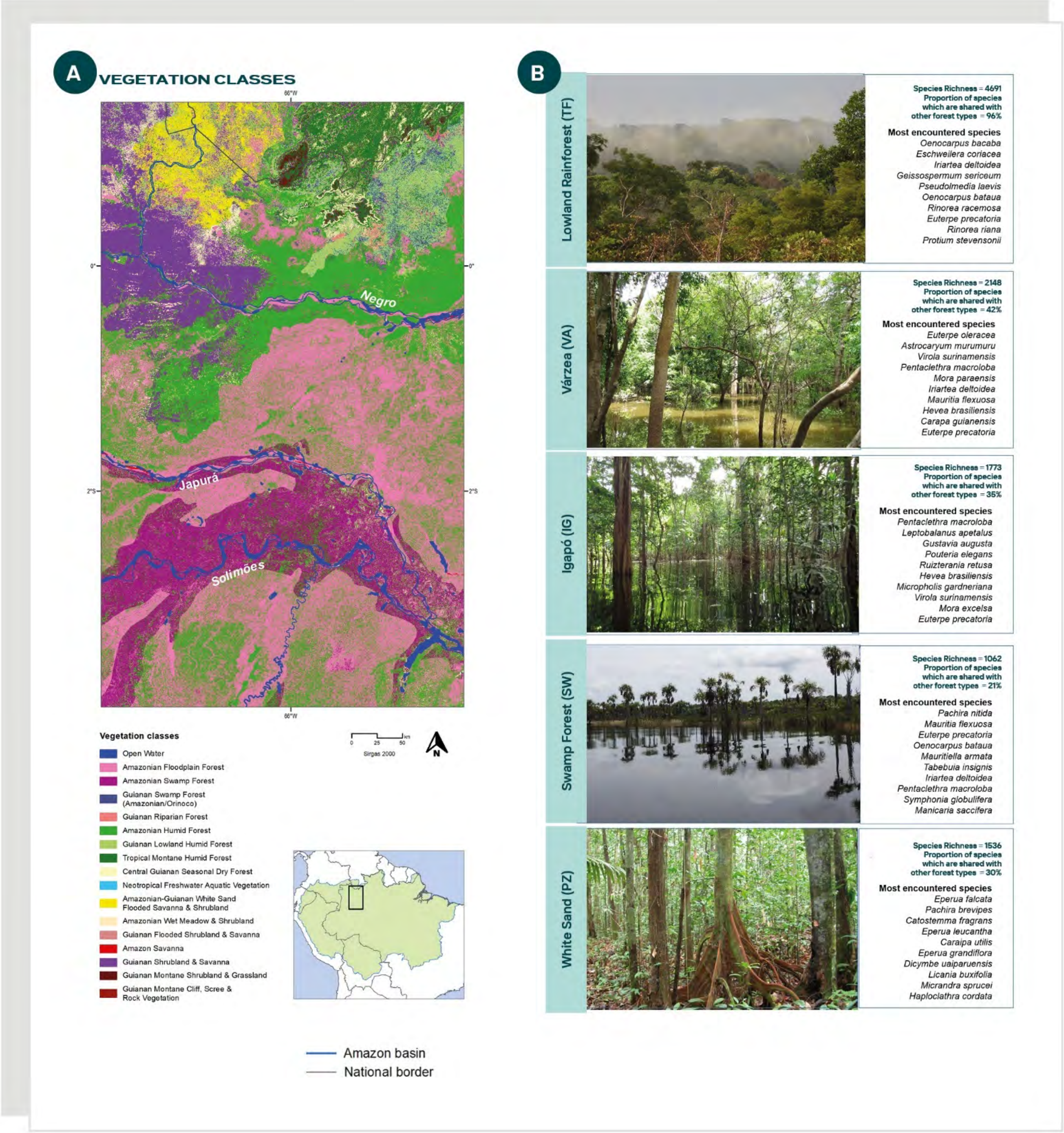


Figure 4.4 A. Key ecosystems are found in Amazonian lowland rainforests, such as floodplain forests, Amazon savanna, white-sand savanna, and seasonally dry forest. B. The ten most encountered tree species on ~2,000 plots across the Amazon by forest type (IG – igapó, PZ – white sand forest, SW – swamp forest, TF – *terra firme* forest, VA – várzea forest. Top lines: total species encountered in plots in these forest systems and the percentage compared to the 5,058 species in all 2,000 plots (data: ter Steege *et al.* 2015).

well as grasses such as *Trachypogon, Paspalum*, Cyperaceae, and others (Pires and Prance 1985).

Among the animal species characteristic of the savannas are the White-Tailed Deer (*Odocoileus virginianus*), Greater rhea (*Rhea americana*), Southern screamer (*Chauna torquata*), Banded armadillo (*Dasypus novemcinctus*), and maned wolf (*Crysocyon brachyurus*).

4.2.2. Fresh Water bodies and Wetlands

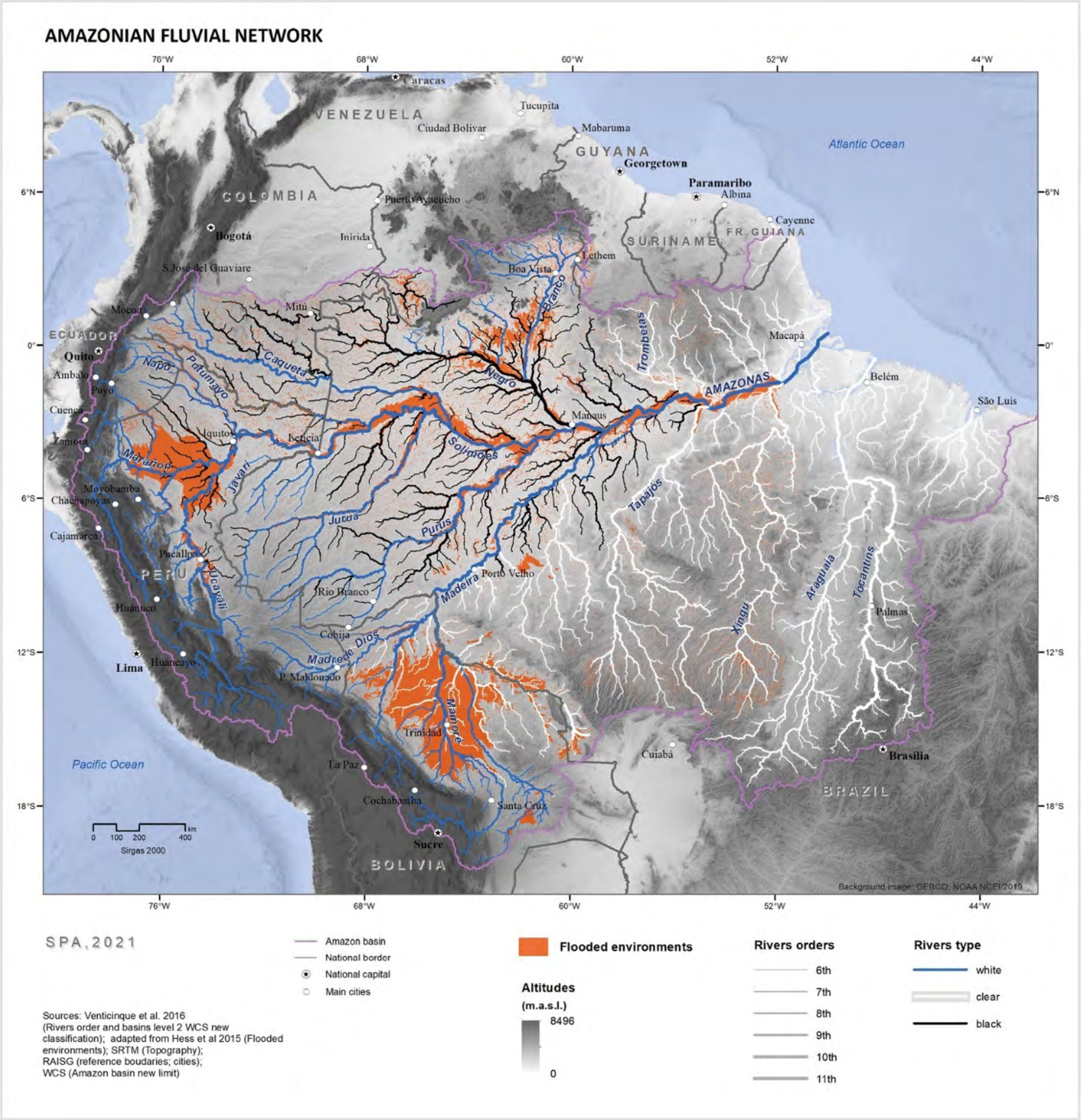
Freshwater ecosystems in the lowland basin (elevations below 500 m) include rivers, lakes, and streams, in addition to areas with permanent, temporary, or seasonal standing or flowing water, or with saturated soils, such as swamps, flooded forests, and marshes. These ecosystems are a fundamental part of the large fluvial system of the Amazon and occupy >800,000 km^2, or 14% of the drainage area (Melack and Hess 2010; Hess *et al.* 2015). Aquatic ecosystems in the Amazon are connected through the annual *flood pulse*, the periodic fluctuation in water level that connects lowland rivers with their floodplains and allows the exchange of water, organic and inorganic materials, and organisms (Junk and Wantzen 2003, Junk *et al.* 2015; see 4.3.2 below). Depending upon classification criteria (e.g., scale, floristic composition, geomorphology, the pattern of inundation, and water chemistry), aquatic ecosystems and freshwater wetlands may vary from a few general types to more than 30 distinctive ecosystems (Comer *et al.* 2020).

4.2.2.1. Rivers, Lakes and Forest streams

The Amazon drainage basin is formed by the Amazon River and approximately 269 sub-basin tributaries with catchment areas between 300-1,000 km^2 (Venticinque *et al.* 2016). The largest tributary systems that join the Amazon are the Madeira, Negro, Japurá, Tapajos, Purus, and other rivers that are among the 20 largest rivers on the planet. With more than 7,000,000 km^2, the Amazon is the most extensive hydrographic network in the world, bordered by riparian forests or swamps, and sustains the greatest freshwater fish diversity on Earth; an ichthyofauna that is equivalent to 15% of all freshwater species currently described (Junk *et al.* 2011, Tedesco *et al.* 2017). In the animal communities associated with aquatic ecosystems there are numerous fish species, and iconic species such as Capybara (*Hydrochoerus hydrochaeris*), Neotropical otter (*Lutra longicaudis*), Giant otter (*Pteronura brasiliensis*), Amazon River Dolphins (*Inia* spp.), Yellow-Spotted River Turtle (*Podocnemis unifilis*), Matamata (*Chelus fimbriatus*), Anaconda (*Eunectes murinus*), Black Caiman (*Melanosuchus niger*), and other species of crocodilians, among others.

The Amazonian fluvial network is made up of different types of waters (Figure 4.5). Amazonian rivers generally are classified into white-water, clear-water, and black-water, based on the color of the water, which is related to transparency, acidity (pH), and electrical conductivity (Sioli 1984, Bogota-Gregory *et al.* 2020, Table 4.1). These water characteristics also correlate to the geological and geomorphological properties of the river catchments and their origins (McClain and Naiman 2008). The catchment properties directly influence the composition and amount of suspended sediments in the water and, in turn, the productivity of rivers and floodplain lakes (Sioli 1984). The fish communities in rivers and associated floodplains also are influenced by water characteristics. Conductivity and turbidity, in particular, seem to be major drivers shaping Amazonian fish communities (Bogota-Gregory *et al.* 2020).

White-water rivers (such as the Amazon main stem, Caquetá-Japurá, Marañón, Ucayali, and Madeira) originate in the Andes, or, in the case of the Jurua and Purus Rivers, in the hilly, rugged moderate elevations below 1,000 m in the Ucayali region in Peru. The Andean mountains supply most of the terrestrial sediments, organic matter, and mineral nutrients influencing the hydrology, geomorphology, biochemistry, ecology, and productivity of white-water rivers and their floodplains, all the way to the Amazon River



Sources: Venticinque et al. 2016 (Rivers order and basins level 2 WCS new classification); adapted from Hess et al 2015 (Flooded environments); SRTM (Topography); RAISG (reference boudaries; cities); WCS (Amazon basin new limit)

Figure 4.5 Amazon River Network across the largest tributary systems and the entire Amazon Basin (source: Venticinque et al. 2016), indicating the distribution of flooded environments (modified from Hess et al. 2015). Wetland areas cover ~14 % of the basin (nor considering Tocantins-Araguaia drainage and estuarine coastal areas) ($5.83×10^6$ km^2) and 16 % of the lowland basin ($5.06×10^6$ km^2) (Hess et al. 2015).

Table 4.1 Ranges of physico-chemical properties in blackwater, clearwater, and white-water for rivers and floodplain lakes across the basin (gray text) (Source: Bogotá-Gregory *et al.* 2020). Conductivity (EC), dissolved organic carbon (DOC), dissolved oxygen (DO), Inorganic (Inorg.), Herbaceous (Herb.). [a] Periodic phytoplankton (including cyanobacteria) blooms induce DO supersaturation (ca. 8–15 mg L^{-1}) and color clearwater green. [b] Precipitation of suspended silt due to reduced flow in white-water floodplain lakes substantially increases transparency relative to the parent white-water rivers. [c] High water hypoxia results from litter decomposition in inundation forests; this effect is greater in large white-water floodplains. [d] Shallow white-water lakes reach extreme high low-water temperatures.

Water Chemistry	Whitewater	Clearwater	Blackwater
pH	High (6.5-7.5) (near neutral)	Intermediate (EC 5.5-8.0)	Low (3.5-6.0) (acidic)
Color	Turbid, Cafe con Leche	Clear or blue-greenish	Reddish or brownish
Nutrient	High (EC 40-300 µS cm^{-1})	Low (EC 5-40 µS cm^{-1})	Low (EC 5-20 µS cm^{-1})
Dominant cations	Na^+/K^+	Variable	Ca^{2+}/Mg^{2+}
Dominant anions	$CO_3^{2-}/NO_3^{-}/PO_4^{3-}$	Variable	SO_4^{2-}/Cl^-
DOC	High	Low	High
Transparency	Low (0.1-0.6 [usually < 0.3] m)	High (1-3 m)	High (0.6-4 m)
	Variable (LW <0.6, HW 0.5-3 m)[b]		
DO[a]	High (2-8 mg L^{-1})	High (2-8 mg L^{-1})	High (2-8 mg L^{-1})
	Variable (LW[c] 2-8, HW[c] 0-3 mg L^{-1})		
Temperature	High (29-32°C)	High (29-32°C)	High (29-32°C)
	Variable (LW 29-34, HW 27-32 °C)[d]		
Inorg. sediment load	High	Low	Low
Sediment type	Fine alluvial silt	Sand	Sand
Sediment fertility	High	Low	Low
Herb. macrophytes	Absent-Sparse	Absent-Sparse	Absent-Sparse
Floodplain forest	Várzea (high-productivity)	Igapó (intermidiate-productivity)	Igapó (low-productivity)

estuary, associated mangroves, and the ocean (McClain and Naiman 2008; Filizola and Guyot 2009; Encalada *et al.* 2019). Andean-derived large sediment loads control downstream channel erosion and width, bed elevations, and the availability of riparian habitats and vegetation. These, in turn, influence the connectivity between river channels and floodplains, and therefore spatial patterns of inundation and floodplain productivity (Constantine *et al.* 2014; Forsberg *et al.* 2017). White-water rivers are turbid, with water transparency ranging between 20 and 60 cm, because the high sediment loads contain suspended clay particles from drained soil and completely degraded plant material. White-water rivers have near-neutral pH, and the relatively high concentration of dissolved solids is reflected in the electric conductivity, which varies between 40–300 µS/cm (McClain and Naiman 2008, Bogota-Gregory *et al.* 2020). White-water rivers are surrounded by diverse *várzea* floodplain forests and extensive floating meadow wetlands (Wittmann *et al.* 2011, see 4.2.2.2. below).

Clear-water rivers (such as the Tapajós and Xingu Rivers) have their upper catchments in the cerrado region of central Brazil and drain the ancient Brazilian shield, which has been strongly eroded over millennia (Sioli 1984). The pH of clear-water rivers varies from acidic to neutral, depending on the soil, and the water hardly carries any suspended and dissolved solids (Sioli 1984). The transparency of their greenish waters is high (100–300 cm), electrical conductivity ranges between 5–40 µS cm, and pH varies between 5.5–8 in large rivers (Bogota-Gregory *et al.* 2020).

Black-water rivers have their origin in lowlands, are translucent, high in dissolved organic carbon, and low in nutrients. Rivers such as the Negro in Brazil and Vaupés and Apaporis in Colombia drain the Precambrian Guayana shield, characterized by large areas of white sands (podzols). Water transparency ranges between 60–400 cm, with low quantities of suspended matter but high amounts of humic acids (rich in dissolved organic carbon (DOC) from the incomplete degradation of forest plant material), which give the water a brownish-reddish color. The pH values are in the range of 3.5–6 and electrical conductivity varies between 5–20 µS/cm (Bogota-Gregory *et al.* 2020). Clear and black-water rivers are surrounded by another type of flooded forest, igapó (See 4.2.2.2. below for a detailed description of Amazonian floodplain wetlands).

Nevertheless, many rivers and streams do not easily fit into these three categories and are considered as “mixed waters”. Greater variability in water biochemistry results from the influence of lower-order tributaries with different biogeochemical water properties that vary seasonally depending on flooding levels and connectivity.

Amazonian lakes are the result of fluvial processes in depressions or flooded valleys. Four main categories are distinguished: 1) lagoons in ancient lands not directly related to river systems (e.g., the Hill of Six Lakes in the northern Amazon), 2) lakes in river valleys and quaternary sediments (not related to geographical features: e.g., Pará and Rondonia states), 3) lakes generated by river processes (e.g., the Boa Vista Formation in the northern Amazon), and 4) "lakes" of wetlands (a mosaic of lakes with a large diversity in origin, shape, and functioning) (Latrubesse 2012). Depending on fluvial processes, two other groups are recognized: 1) lagoons formed by the lateral displacement of the channel, in stretches of abandoned channels and meanders (lagoons or swamps depending on the degree of sedimentation), and lagoons that join islands to the floodplain; and 2) lakes generated by geographical features such as those built by vertical accretion processes in the main channel and by floods in the alluvial plain (e.g., square lagoons also influenced by tectonics in SW Amazon), or by deltas of alluvial plains, with dikes and blocked valleys (e.g., ria lakes).

In meandering rivers such as those found in the Amazon Basin, sediment deposits rich in clay form within floodplains. These clay deposits slow water flow and thus help to decrease the migration rates of the channel – up and down streams – affecting bank erodibility on a large scale (10–50 km) and sinuosity by 30% (Schwendel *et al.* 2015). The grain size of clay-rich sediment deposits is similar to that of deposits near the outlet of a meandering lake (1.5–3.0 µm) and form clay plugs (Gautier *et al.* 2010). The abandoned meanders of rivers are known as oxbow lakes that may or may not recover the sinuosity of the river. However, while stagnant waters remain, aquatic submerged plant communities rapidly colonize floodplain lakes, including species such as *Victoria amazonica, Lemna* spp.*, Nymphaea gardneriana,* and *Eichhornia* spp., among others. Oxbow lakes of black-water rivers are typically free of aquatic plant communities due to their low nutrient levels.

Few areas within the lowland Amazon are more than 100 m above the river, where water comes to the surface in the form of a dense network of small streams. Most stream fauna depends on energy inputs from the surrounding forest (e.g, insects and plant material) and much of the terrestrial flora and fauna also depend on resources from streams. Intricate connections between aquatic and terrestrial ecosystems continue as the streams coalesce to form larger rivers. In general, small streams are considered part of the *terra firme* forest ecosystem and harbor great aquatic biodiversity (Arbelaez *et al.* 2008). However, as they form larger rivers, the forest canopy is no longer continuous, instead, the floodplain areas around rivers support extensive forests (see 4.2.2.2. below), and the terrestrial and aquatic ecosystems become more distinct (see 3.2. below).

4.2.2.2. Freshwater Wetlands

There are several definitions of wetlands, but a broad and simple definition is proposed by Junk *et al.* (2011, 2014), which states that "wetlands are ecosystems at the interface between aquatic and terrestrial environments with biota adapted for life in water or in water-saturated soils." Recent large-scale mapping efforts have identified numerous wetlands dominated by vegetation, in different sub-basins of the entire Amazon Basin. If we consider small riparian wetlands and waterlogged savannas and grasslands, the estimated area covered by wetlands extends to 2.3 million km^2 or 30% of the basin (Junk *et al.* 2011). Wetlands are divided into two main groups: 1) those with relatively stable water levels (e.g., *Mauritia flexuosa* palm swamps), and 2) those with oscillating water levels (e.g., floodplain forests, mangroves). Some of these wetlands are forest-dominated and broadly distributed. In contrast, others are emblematic as they represent specific regions within the basin, such as savanna ecosystems in the Llanos de Moxos, located in the Madeira basin of Bolivia; Bananal savannas of Brazil which are seasonally inundated grasslands, sedgelands, and open woodlands among many others (Castello *et al.* 2012, Figure 4.1). In the Upper Negro river basin, the Amazonas Savannahs Refuge and parts of the Imeri Refuge are considered centers of endemism for floodplain tree species, such as *Mauritia carana*, *Ocotea esmeraldana*, and *Vitex calothyrsa* (Junk *et al.* 2010). All of these wetlands are vital to support local communities' livelihoods.

Floodplain Forest Seasonally flooded forests are second in area to *terra firme* forests (0.76 million km^2, 10%), and subjected to predictable, long-lasting, annual flood pulses (Junk *et al.* 2011; also see 4.3.2. below). These forests are flooded due to their low topographic location and poorly drained soils. Flooding may last up to six months and water levels may fluctuate up to 10 m between the dry and flood seasons (Schöngart and Junk 2007). The timing, duration, and magnitude is variable across the basin. Such temporal and spatial variation is mostly driven by air circulation patterns and headwater precipitation modulated by the Intertropical Convergence Zone and topography (Siddiqui *et al.* 2021). Although these forests are flooded annually, different floristic zones are distinguished, which are influenced by the input of sediments and nutrients in river waters, flood regimes, and hydro-geomorphic dynamics (Prance 1979, Wittmann 2010).

Floodplain forests along white-water rivers are known as *várzea* in Brazil (or *rebalse* in Colombia) and represent the most extensive type of flooded forest in South America, covering approximately 0.46 million km^2 of the Amazon Basin (Junk and Wittmann, 2017). Amazonian white-water river floodplain forests contain around 1,000 species of trees, making them the most diverse floodplain forests in the world (Ferreira and Prance 1998; Wittmann *et al.* 2002, 2006). A significant number of tree species are almost entirely restricted to the floodplain (~40% of the most common central Amazonian *várzea* tree species), while only ~31% of tree species in *várzea* are shared with *terra firme* forest (Wittmann *et al.* 2011). Due to the seasonal influx of nutrients carried by white-water rivers, floodplain forests are eutrophic and highly productive (Junk and Piedade 1993), but their flora and fauna diversity is less than that of *terra firme* forest (Patton *et al.* 2000; Haugaasen and Peres 2005a, b). This is because of the selective pressure imposed by prolonged annual floods. Due to its high productivity, *várzeas* have been important centers of human colonization which have intensified in the last thirty years (Piedade *et al.* 2010). Data on the productivity of Amazonian aquatic ecosystems are relatively few, but those available show that remarkably high values are locally possible. This is likely due to the combination of abundant nutrient and water supply, insolation, and macrophytes adapted to rapidly occupy the water-atmosphere interface when conditions permit (Table 4.2). The floodplain forests of Brazil, Peru, and Ecuador are characterized by the presence of families such as Fabaceae, Moraceae, Are caceae, Lecythidaceae and Annonaceae (Nebel *et al.* 2001) and the flooded period may vary from 1 or 2 months to 6 months. In *varzeas* of the central Amazon, characteristic tree species include *Ceiba pentandra, Hura crepitans, Nectandra amazonum,* and *Cecropia* spp. (Worbes 1997). These species represent the early sequence forest species, have low wood density, and make up the successional process which is governed by hydrological seasonality. Tree density (at 10 cm dbh) in *várzea* varies along successional stages and flood-gradient position (i.e., high and low *varzeas*), being in average 400–500 individuals ha^{-1} and with highest values occurring in early-secondary stages (800–1,000 individuals ha^{-1}) (Wittmann *et al.* 2011).

There are also floodplain forests along black-water rivers (Junk *et al.* 2011), called *igapó* in Brazil. The *igapó* forests are seasonally flooded by black (or clear) water rivers, for up to 9 m in depth, and cover around 302,000 km^2 (Melack and Hess, 2010; Junk *et al.* 2011). Due to the lack of soil nutrients, tree abundance and biomass in *igapó* forests is much lower than in *várzea* and *terra firme* forests (Ferreira 1997, Junk *et al.* 2015, Wittman and Junk 2017). Montero *et al.* (2014) recorded 6,126 trees with 243 species, 136 genera, and 48 families in 10 hectares along the middle Rio Negro. Most species found in *igapó* also occur in other ecosystems, such as *terra firme* and *várzea* forests, savanna, swamps, or white-sand forests (Junk *et al.* 2015). Among herbs, 55 species have been documented, belonging to 20 families (Lopes *et al.* 2008); most of the species were found with an exclusively terrestrial habit in the *igapó* and belong to two main families: Cyperaceae (45% of the total) and Poaceae (7.3%) (Piedade *et al.* 2010).

In general, comparison between *terra firme*, *várzea* and *igapó* forests shows differences in tree richness (Figure 4.4) and structural trends in the number of individuals. In general, *terra firme* forest shows greater density and richness of large trees (diameter at breast height ≥ 10 cm), followed by *várzea* and *igapó* forests.

Permanently Flooded Swamps Permanently flooded or waterlogged areas (swamps) occupy a small area compared to other ecosystems in the Amazon (80,000 km^2, 1%). The extensive palm

Table 4.2 Net primary production (NPP, dry weight) for the most important populations and communities of aquatic herbaceous plants in central Amazon *várzea*. NPP was measured under different methods and assumed to have a monthly loss between 10 and 25% of the biomass (Source: Piedade *et al*. 2010).

Population/Community	Maximum NPP (t.ha^{-1})	Time for production (months)
Monospecific stands of *Echinochloa polystachya* (Kunth) Hitchock¹	100	12
Monospecific stands of *Paspalum fasciculatum* Willd.²	70	7.7
Mixed populations dominated by *Hymenachne amplexicaulis* (Ruudge) Nees²	48	9.5
Monospecific stands of *Paspalum repens* P.J. Bergius²	33	4
Monospecific stands of *Oryza perennis* Moench²	27	4
Mixed populations dominated by *Oryza perennis* Moench²	17.5	5

formations of *Mauritia flexuosa, Oenocarpus bataua*, and *Euterpe oleracea* (Arecaceae) are very characteristic of swamps of the Amazon. Their distribution is azonal as they are found from the lowland plain to the Andean foothills, up to 500 m of altitude, always associated with highly stagnant black-waters (Moraes R *et al.* 2020), such as in permanent wet depressions within the savanna landscape (*Mauritia flexuosa*) (Junk *et al.* 2010). There are also permanent swamp areas with rooted plants in channels or depressions within the alluvial plain, characterized by herbaceous species including *Cyperus giganteum, Thalia geniculata, Pontederia* spp., *Eichornia* spp., among others (Pires and Prance 1985; Beck and Moraes R 1997).

Flooded Savanna The seasonally flooded savannas of the alluvial plain cover an area of ca. 200,000 km^2 (Pires and Prance 1985) and represent 6% of flooded plant communities (Meirelles 2006). They occur in the northern (Roraima and Rupununi) and southern (Beni savanna) Amazon, along the cerrado belts in Brazil and the Guianas, and have strong climatic seasonality (several dry moths) (Junk *et al.* 2011).

Flooding is mainly influenced by rainfall and the overflow of rivers during 3-5 months of the year, but in a matter of hours, the flooding percolates and the landscape returns to its natural state without permanent water, except in lower places and in depressions linked to rivers. On alluvial plains of white-water rivers, Poaceae species predominate (32% of the total), followed by Cyperaceae (20%) (Junk and Piedade 1993), and their contribution to net primary production (NPP) make them the most important aquatic herbaceous plant community (Piedade *et al.* 2010).

Flooded savannas and grasslands are very fragile ecosystems. Savannization processes are being generated by the reduction of floodplain forests due to various dynamics, such as deforestation and fires driven by severe droughts in minimally flooded regions. Such ecosystem shifts favor grasslands and deteriorated aquatic communities, as was demonstrated in the Pantanal which is considered a hyper-seasonal savanna (Nunes da Cunha and Junk 2004).

Mangroves Mangroves occupy relatively small areas in a narrow littoral belt towards the Atlantic Ocean and in the Amazon estuary. Mangroves are subject to flooding by salt water or brackish water and have only a few tree species, generally uniform in structure, not exceeding 10 m in height. The dominant mangrove species (in order of abundance) are *Rhizophora mangle* (common names are mangue verdadeiro in Brazil, red mangrove elsewhere), *Avicennia nitida*, and *Laguncularia racemosa* (Pires and Prance 1985, Junk *et al* 2010). Brazilian mangroves occur mostly along the coasts of Amapá, Pará, and Maranhão states and cover an area of about 14,000 km^2 (ICMBio 2018). The largest mangrove area extends southward from Belém and measures at least 7,000 km^2 (FAO 2007; Menezes *et al.* 2008). Little is known about the wetlands along the coastline north of Belém. For Guyana, Huber *et al.* (1995) estimated that there are about 900 km^2 of coastal mangroves. In areas with very strong freshwater influence near the Atlantic coast, *várzea* forests may replace mangroves.

4.3. Ecosystem Functioning

4.3.1. Primary productivity, nutrients, forest dynamics and decomposition

4.3.1.1. Terrestrial ecosystems

In the Amazon, climatic factors exert the greatest influence on gross production (GPP) in terrestrial ecosystems, but a wide range of other factors related to soil, forest disturbance, and species composition are also influential in determining how captured carbon is allocated and how long it is stored in tree woody biomass and other ecosystem compartments. Thus, bottom-up studies of the carbon budget and its seasonal variation using intensive measurements in plots of the GEM

(Global Ecosystems Monitoring) network (Malhi *et al.* 2021) show variation in GPP between sites from around 33 to 38 Mg C ha^{-1} yr^{-1} for more humid forests (in the west and north) to lower values of 25 to 30 Mg C ha^{-1} yr^{-1} in drier forests of the Brazilian Shield and central Amazon (Malhi *et al* 2015). However, carbon-use efficiency (CUE), defined as the fraction of fixed carbon that is used to produce plant matter, i.e. NPP divided by GPP, appears to be lower (0.3 – 0.4) in wetter sites than in more seasonal sites (0.4 – 0.5). Overall, the decline in GPP in the drier sites is compensated by shifts in CUE and in allocation, so that in these studies there is often no clear decline in tree woody growth toward more seasonal parts of the Amazon. Compensatory shifts in CUE and allocation unrelated to climate thereby may effectively decouple spatial variation in GPP, NPP, and woody growth.

Less intensive but more extensive measurements of woody growth and tree mortality (Box 4.1), combined with species composition and soil measurements, help confirm the role of non-climatic factors in affecting how carbon is allocated in Amazonian ecosystems. In the widespread RAINFOR forest inventories, above-ground woody production is more closely linked to edaphic factors, such as phosphorus concentrations, than to climate (e.g., Quesada *et al.* 2012). Other non-climate factors play a role too. Thus, the high tree mortality rates of some Amazonian forests as a result of wind-disturbance (e.g., Esquivel Muelbert *et al.* 2020), while the poor physical structure and shallow rooting depths of many western Amazonian soils (Quesada *et al.* 2012), ensure that more forest here is naturally in early to intermediate successional states. These tend to produce wood faster and may have greater carbon use efficiencies (Rödig *et al.* 2018). Additionally, the nature of the species present makes a difference too; where tree phylogenetic diversity is greatest, forests have greater levels of woody productivity, even accounting for covarying climate and edaphic factors (de Souza *et al.* 2019). There is also evidence that animals may increase nutrient cycling and subsequently the productivity of the forest (e.g., Sobral *et al.* 2017), and it is possible that the pre-Colombian extinction of Amazonian megafauna has impacted productivity negatively by slowing the nutrient transfer from richer floodplains to hinterland *terra firme* forests, a function which the original large herbivores would have performed (Doughty *et al.* 2016).

What does all this mean for forest dynamics, biomass, and carbon storage? Inventory plots show that differences in above-ground biomass track more closely to underlying edaphic factors than to climate factors.

Mortality rates vary greatly across the Amazon, being higher in the western and southern regions, around 2.2-2.8% per year, than in the northern and eastern central regions where 1.1 - 1.5% is typical (Phillips *et al.* 2004, Marimon *et al.* 2014, Esquivel *et al.* 2020). Fast turnover forests often correspond to where soils are relatively rich chemically but offer poor structural support physically. Associated with these high rates of stand-level tree mortality is the prevalence of species with ‘live-fast-die-young’ life-history strategies that tend to favor growth over survivorship, with lower wood density storing less carbon (Baker *et al.* 2004, ter Steege *et al.* 2006, Honorio Coronado *et al.* 2009, Patiño *et al.* 2009).

Remarkably, basal-area weighted wood density in the slow-turnover forests of the northeast Amazon is up to 50% greater than in fast-turnover forests in the south and west (Phillips *et al.* 2019). In sum, three decades of careful observation in permanent plots shows that spatial variation in Amazonian biomass carbon stocks and dynamics are driven more by soil conditions than climate, and more by spatial variation in mortality than productivity. These findings run counter to the dominant paradigm in ecosystem vegetation models which has emphasized the role of climate and processes of carbon *production* (GPP, NPP, tree growth), rather than its turnover and *loss* (especially mortality), and which often ignore the physical constraints and floristic compositional

BOX 4.1 How much does the longevity of Amazonian species vary?

Tree age has generally been inferred based on trunk diameter growth rates (growth rings) (Figure B4.1A)., mortality (Condit *et al.* 1995, Shöngart *et al.* 2015), or radiocarbon dating (^{14}C) (Chambers 1989, Vieira *et al*. 2005). The maximum longevity values based on demographic studies were inferred in 93 species of canopy trees in the rain forest in the Central Amazon, considering the influence of the life cycle, such as wood density, growth form, mortality rate, rate of recruitment, trunk diameter, increase in growth, and population density. Maximum longevity ranged from 48 years for the pioneer tree *Pourouma bicolor* (Cecropiaceae) to 981 years for the canopy tree *Pouteria manaosensis* (Sapotaceae), with an overall average of 336 ± 196 years (Laurance *et al*. 2004). These estimates of tree maximum age coincided with the analyses of the average mortality rates; the longevity of the tree was positively correlated with the density of the wood, the maximum diameter of the stem, and the population density, while it was negatively related to annual mortality, recruitment, and growth rates; pioneer species had much shorter longevity than climax trees (Laurance *et al.* 2004).

Tree age data provide important information for conservation and sustainable forest management. Emergent old-age trees in the central Amazon, for instance, represent a key component of the forest's carbon budget, as around 50% of the aboveground biomass is retained in less than the 10% of the largest trees (Chambers *et al.* 1989). The time required for a tree to achieve a certain diameter varies with

Figure B4.1 (A) Stem disk, and Tree rings of *Bertholletia excelsa* Bonpl. (Lecythidaceae) from a plantation tree in Manaus. Tree rings are defined by an alternating pattern of fiber (dark tissue) and parenchyma (light tissue) (Shongart *et al.* 2015, ©Wiley). (B) *Bertholletia excelsa* achieves 50 meters' height tree in terra firme forests and 400 years of age (© WWF-Brazil / Clóvis Miranda).

BOX 4.1 *continued*

radial growth rates, with the cambial activity being influenced by abiotic site conditions and precipitation that limits water in the dry season (Worbes 1999). *Bertholletia excelsa* (Lecythidaceae), a tree of 50 m height, may have 400 years and a diameter of 150 cm (Figure B4.1). As growth is higher under favorable light conditions (e.g., under canopy gaps), a tree of 10 cm diameter can have an age varying from 13 to 50 years (Shöngart *et al.* 2015). The flood-tolerant tree *Calophyllum brasiliense* (Calophyllaceae) may achieve a maximum age of 490 years in a black-water floodplain. Under permanently waterlogged conditions the longevity is reduced to 72 and 134 years. As consequence, for achieving the 50 cm diameter-cutting limit based on forest management norms in the Brazilian Amazon, *C. brasiliense* would spend 70 years in white-river floodplains, but a remarkable 400 years in black-water floodplains (Rosa *et al.* 2017), suggesting habitat-specific Growth-Oriented Logging is needed to ensure species conservation (Schöngart 2008).

The relation between radial growth rates and precipitation in the Amazon floodplain allows an estimate of the effect of climate variability induced by the El Niño phenomenon with forest dynamics. Low precipitation events influenced by El Niño (see Chapter 22) are related to increased growth periods in the long-living (143 to 289 years old) hardwood species *Piranhea trifoliata* Baill. (Picrodendraceae). Unlike in *terra firme* forests, the influence of drought on growth rates in floodplain trees may increase carbon absorption, partially compensating the carbon emitted from *terra firme* forests under El Niño periods (Shongart *et al.* 2004). Efforts to determine the age and growth rate of tropical trees under flooded and non-flooded conditions, and the influence of climate and soil conditions on growing patterns, are essential to guide wise use and long-term preservation (Vetter and Botosso 1989, Shöngart *et al.* 2008).

factors which largely determine Amazonian forest biomass.

The key effects of soils on Amazonian ecosystem function extend also to animals and their important functions, including herbivory and seed dispersal. Travelers from the west to the east of the Amazon are often struck by the remarkably low level of insect activity, which can make fieldwork much more comfortable. This likely reflects fundamental controls of cations and other nutrients on the metabolism of animal consumers (e.g., Kaspari *et al.* 2009) as well as plant producers (e.g., Lloyd *et al.* 2015). In the white sand forests of the Amazon, the interaction of impoverished soils and herbivory can select for investment in defense by the plants, while in forest formations with clay soils species are instead favored that commit resources to rapid growth (Fine *et al.* 2006). Large animals too respond to bottom-up soil controls; for example, Stevenson *et al.* (2016) found that Neotropical primate abundance and diversity are largely controlled by fruit production, and with much greater biomass and diversity in the western Amazon than in the Guiana and Brazilian Shields. Such effects are likely to extend to many other animal groups, as we have known for more than a third-of-a-century that production of flowers and fruits in the neotropics is closely tied to soil nutrient status (Gentry and Emmons 1987).

Finally, we note that climate nevertheless does impact rates of woody production, and clearly has consequences for forest carbon storage and biodiversity. Both worldwide and in the Amazon, woody production is suppressed in the most extreme seasonal tropical forest climates with high maximum temperatures and high seasonal water deficits (Sullivan *et al.* 2020). This means that some Amazonian forests are already at the climatic limits capable of sustaining productive forest ecosystems. As a consequence, in some of the tropical forests which have warmed and dried most, the long-term carbon sink of a mature forest appears to have recently weakened (Hubau *et al.* 2020). In the Amazon we also know from long-term RAINFOR plots that forest composition is being affected by recent droughts, with the mortality of wet-affiliated genera increasing in places where the dry season has intensified most (Esquivel Muelbert *et al.* 2019). However, not all Amazonian forests appear to be so impacted, with large areas with shallow water tables in the central and western Amazon potentially effectively immunized against drought via local water supplies, in some cases even seeing an increase in growth and carbon stocks during recent drought (Sousa *et al.* 2020). Key areas of scientific uncertainty include the extent to which recent climate change has actually caused the slowdown in the intact Amazonian biomass carbon sink (Brienen *et al.* 2015), and whether it might soon go into reverse, with the remaining intact Amazonian forests becoming a net carbon source under further warming, as some have predicted (e.g., Hubau *et al.* 2020, Sullivan *et al.* 2020). Alternatively, forests may prove more climate-change resistant than expected, especially if the shallow water tables, wetter climates, and rich biodiversity of many Amazonian forests, in the west especially, help prevent large regions of the Amazon from becoming a net carbon source. Critical, of course, to the fate of the intact forest sink will be whether the forests themselves survive. A recent analysis shows that for parts of the eastern Amazon carbon losses from deforestation and degradation already exceed the sink in remaining forest lands (Gatti *et al.* 2021).

To complete our picture of forest dynamics, we need to understand the decomposition of dead organic material as a fundamental biogeochemical process, both through its role in the forest carbon (C) cycle and, perhaps more importantly, through its role in the recycling of nutrients to soil and plant communities. Any changes in decomposition processes will have profound impacts on the rate and pattern of nutrient cycling, and hence on forest plant and faunal community dynamics. In elevation gradients at the Andes-Amazon interface in Peru, temperature is the variable that best explains variations in litter decomposition rates (Salinas *et al.* 2011). Pinto *et al.* 2018 indicate that, as an effect of global change, increases in temperature and dry season duration are anticipated for the southern Amazon Basin and the Pantanal (Gatti, *et al.* 2014; Junk 2013), so these are likely to induce changes in decomposition rates and patterns. Also, the physiological, morphological, and biochemical characteristics of Amazonian tree species (their functional traits) play an important role in their decomposition. Species type has a large influence on the decomposition rate (k) (Hättenschwiler *et al.* 2011), most probably through its influence on wood density and leaf quality and morphology. For example, the influence of leaf anatomy is manifested primarily through spongy parenchyma thickness, which strongly influences the moisture-holding capacity of the leaf material, which in turn largely explains the observed moisture content in the leaves.

4.3.1.2. Freshwater ecosystems

As with terrestrial ecosystems, the functions of aquatic ecosystems comprise biochemical activities of productivity (plants and algae), decomposition of dead organic matter, and processes related to the flow of energy and nutrient recycling (Morris 2010). These functions affect and are affected by interactions between living organisms and consecutively sustain biodiversity and human well-being. However, unlike terrestrial ecosystems, the flow of water makes aquatic ecosystems highly dynamic in both space and time. This is due to changing physical conditions and biotic components along stream and river channels, from the headwaters to downstream confluence with other rivers or the sea, and the influence of precipitation on streamflow.

The flow of energy and nutrient recycling are prime examples of the dynamic nature of aquatic ecosystems, and the Amazon is no exception.

Headwater and forest streams are shaded by vegetation, inhibiting algae growth, a key energy producer in aquatic ecosystems. Instead, riparian vegetation subsidizes aquatic food webs that are dominated by shredder invertebrates and decomposer bacteria that help recycle nutrients (Vannote *et al.* 1980). Nutrients travel downstream in a spiral-like pattern and, as the width of the river channel expands downstream, algae growth is no longer limited by shading (Vannote *et al.* 1980). The lack of dissolved nutrients limits algae production in nutrient-poor rivers such as Amazonian clear-water and black-water rivers, while acidity and low light penetration in dark-stained water further limits productivity in black-water rivers. In turbid white-water rivers, light penetration also is a limiting factor to algae growth (Moreira-Turcq *et al.* 2003; Dustan 2009). By connecting rivers with floodplain habitats, the *flood pulse* provides a mechanism to compensate for limited in-situ algal productivity by replenishing nutrients during the annual flood (Junk and Wantzen 2003, see 4.3.2 below).

Some wetlands contribute to carbon storage at a global scale due to the extensive and deep accumulation of below-ground peat deposits. Peat is a type of soil with a top layer composed of at least 50% decomposed or semi-decomposed organic material (i.e., 29% carbon content), extending at least 30 cm deep (Gumbricht *et al.* 2017). Several factors are essential in determining the location of peatland ecosystems, including high rainfall, frequent flooding, low drought and fire frequency, and a low-lying topography that creates waterlogging and anoxic conditions for peat accumulation (Draper *et al.* 2014). Peatland ecosystems also are influenced by different types of waters, with a gradient of nutrient content. They can be nutrient-poor ombrotrophic bogs if they are dominated by atmospheric water, or they can be nutrient-rich swamps that are influenced by rivers (Lähteenoja and Page 2011). For example, in the Pastaza-Marañon foreland basin located in the western Amazon in Peru, an area of 35,600 ± 2,133 km^2 contains 3.14 (0.44–8.15) Pg C below palm swamps. At the same time, peatland pole forests represent the most carbon-dense ecosystem (1,391 ± 710 Mg C ha^{-1}) in the Amazon (Draper *et al.* 2014). Our knowledge here is incomplete, and peat may extend up to nine meters deep (Householder *et al.* 2012). Recent intensive fieldwork revealed 61% more area of peatland pole forest in north Peru than initially thought (Coronado *et al.* 2021, Honorio *et al.* 2021). Because peatland ecosystems function as carbon sinks, they play a crucial role in maintaining the natural balance of the carbon cycle, modulating global warming. Recent models estimate that 38% of Amazonian wetlands form peat deposits; however, the lack of climate data needed to build hydrological models hinders quantification of the true extent of peatland ecosystems within the Amazon basin, and thus the importance of the region in the global greenhouse gas budgets (Gumbricht *et al.* 2017).

4.3.2. The Flood Pulse and Aquatic-Terrestrial Transition Zone

Variation in water flow and depth is driven by regional and local precipitation patterns, which, coupled with variations in stream order, latitude, and elevation across the enormous Amazon Basin, create distinctive flow regimes (Goulding *et al.* 2003, Siddiqui *et al.* 2021). In a recent classification, Siddiqui and collaborators (2021) identified 6-7 flow regimes based on a combination of hydrological characteristics that include the timing of the wet season, the magnitude of change in streamflow, and the number of times streamflow changes from rising to falling within a year. The timing of maximum flow, for instance, changes spatially across the Amazon basin, with maximum flooding occurring in February-March in the southern tributaries and June-July in the northern tributaries. The magnitude of change in streamflow increases in lower elevation areas, while at the same time, the frequency is reduced to a single large flood episode. Rainfall in the headwaters of large Andean rivers causes a *flood pulse* that travels downstream and leads to a predictable annual hydrological cycle with distinct water-level periods (rising, flood, falling, and dry) and long-lasting flooding (4-15 m in depth and weeks to months in duration) in floodplains of lowland rivers (≤ 500 m). This *flood pulse* drives multiple physical, biological, and ecological processes in the Amazon Basin, from sediment transport to fish migration. In addition, the *flood pulse* drastically transforms the landscape of lowland rivers by creating an aquatic-terrestrial transition zone (ATTZ) that allows the movement of nutrients and organisms between river channels and floodplain habitats (Junk and Wantzen 2003).

Interactions between terrestrial and aquatic components are among the most important processes of Amazonian ecosystems. Floodplain wetlands controlled by the seasonal *flood pulse* of white-water rivers are probably the best-documented examples of the importance of ATTZ in the Amazon basin (Junk 1984). These Amazonian floodplains, which are among the most productive natural systems on Earth, originate from the accumulation of large sediment loads drifting from the Andes, fueled by their associated nutrients (Junk 1984; Melack and Forsberg 2001; McClain and Naiman 2008). Complex floodplain macrophyte and forest communities have adapted to these seasonal sediment fluxes and year-round lateral exchanges between the main channel of rivers and their floodplains.

Terrestrial primary production, organic matter, and nutrients captured when floodwaters invade the floodplains decompose or are consumed by organisms become the basis of the aquatic food chain (Junk 1984; Melack and Forsberg 2001). Part of this productivity goes back to the river's main stem through the many organisms that move between the floodplains and the river, including large numbers of fishes during massive annual migrations (Goulding 1980, 1993). Floodplains play crucial roles as feeding grounds and nursery areas for many fishes (Lima and Araujo-Lima 2004; Castello *et al.* 2015, 2019). For instance, most commercially important fishes supporting large fisheries in the Amazon basin are detrivore, herbivore, and omnivore species performing annual lateral migrations into the white-water floodplain habitats that largely contribute to their productivity (Junk *et al.* 1984; Bayley and Petrere 1989; Bayley 1995; Goulding *et al.* 1996, 2019; Isaac *et al.* 2016). In floodplain lakes connected to white-water rivers, the lack of currents allows sediment settling and greater water transparency, facilitating phytoplankton growth and fueling a zooplankton-based food web. Thus, floodplain lakes play a key role as nurseries and feeding grounds to juvenile fish of commercial value (Oliveira 2006). The current consensus among researchers is that a mixture of carbon generated in seasonally available floodplain habitats by algae, forest vegetation, and aquatic plants plays a pivotal role in subsidizing aquatic food webs and commercial fisheries across the Amazon (Benedito-Cecilio *et al.* 2000, Santos *et al.* 2017, Correa and Winemiller 2018).

Massive annual fish migrations transfer a small portion of Andean-derived energy and nutrients from the white-water floodplains to the nutrient-poor black- or clear-water tributaries (see details below). Another perfect illustration of the intimate ecological interactions between the aquatic and terrestrial systems is the ancient mutually beneficial co-evolution and co-adaptation between trees and fishes in Amazonian floodplains. Most tree species produce fruit during the high-water season when fish invade the flooded forest (Ferreira *et al.* 2010; Hawes and Peres 2016). Hundreds of fish species have evolved frugivory habits and may have been the first vertebrate seed dispersers in the Amazon (Goulding 1980; Correa and Winemiller 2014; Correa *et al.* 2015a). They eat fruits falling in the water from floodplain trees and disperse their seeds over long distances, improving their germination and thereby contributing to the maintenance of the flooded forest (Goulding 1980; Kubitzki and Ziburski 1994; Waldhoff *et al.* 1996; Correa *et al.* 2015a, b). In addition to fruits, fish also consume copious amounts of invertebrates that undergo vertical migrations toward the forest canopy during the flood season. The consumption of leaf-eating insects and carnivorous invertebrates that, in turn, predate upon leaf-eating insects creates an indirect feeding link between fish and trees. Whether directly or indirectly, flooded forests provide a critical terrestrial subsidy to riverine fishes, particularly in nutrient-poor black- or clear-water rivers (Correa and Winemiller 2018).

The flood pulse influences multiple aspects of fish reproductive strategies, including fecundity (number of eggs), age at first reproduction, number of reproductive episodes per year, and parental care (Tedesco *et al.* 2008). As a result, changes in water levels affect fish species differently, and fishing yields can lag 2-3 years. The *flood pulse* also affects the movement patterns of terrestrial animals between floodplain and adjacent *terra firme* forests. During the flood period, abundant fruits attract frugivorous monkeys to floodplain forests, while kingfishers track fish movement to the interior of flooded forests. During the dry period, seedling germination drives the movement of terrestrial animals to floodplain forests, while hummingbirds take advantage of the synchronicity in flower production (Haugaasen and Peres 2007, Beja *et al.* 2009). Moreover, flooding enhances habitat heterogeneity in floodplain forests, which influences the formation of unique bird, bat, and amphibian communities not found in adjacent *terra firme* forests (Beja *et al.* 2009, Pereira *et al.* 2009, Ramalho *et al.* 2018).

4.4. Conclusions

The Amazon biogeographical region covers ~7 million km^2, 5.79 million km^2 of which are lowland tropical rainforests. We have shown that as well as climate, soil has a powerful influence on species richness and composition and on forest function. Based primarily on the geological age of parent material and soil nutrients, the Amazon can broadly be divided into six regions (Figure 4.3).

The total species richness of the Amazon is still actively debated. A well-supported estimate for trees (diameter >10 cm) is 16,000, of which ~10,000 have been collected there. Estimates of the total flora range from 15,000 – 55,000. As in other tropical areas, Fabaceae (the bean family) is the most abundant and species-rich of all woody plant groups. South America and the Amazon are also renowned for their great abundance and richness of palms.

The Amazon region holds the largest tropical wetland system on Earth, home to 15% of all known fish species (see Chapter 3, Jézéquel *et al.* 2020).

Its rivers are classified as white-water (rivers carrying sediments from the Andes); clear-water (draining the two shield areas); and black-water (draining the white sand areas). The water type determines the forest type along the rivers, with *igapó* forest growing in sediment-poor clear and black-waters floodplains, and *várzea* floodplain forests in white, sediment-rich waters. The physical-chemical characteristics of the different water types, particularly electrical conductivity and turbidity are major factors shaping fish communities in rivers and associated floodplains. The *flood pulse* causes marked periods of floods and droughts, which drive physical, biological, and ecological processes, from sediment transport to fish migration, and together with the elevational gradients in the floodplain are factors that favor the maintenance of various plant communities. The white-water wetlands are probably the best-documented examples of the importance of the aquatic-terrestrial transition zone and among the most productive systems on the planet.

Variation in gross primary productivity between forest sites ranges from 33 to 38 Mg C ha^{-1} yr^{-1} for more humid forests (in the west and north) to lower values of 25 to 30 Mg C ha^{-1} yr^{-1} in drier forests of the Brazilian Shield and central Amazon. It is also partly driven by soil characteristics. Climate nevertheless also impacts the rate of wood production, and the prevailing baseline climate has consequences for forest carbon storage and biodiversity. Both worldwide and in the Amazon, wood production is suppressed in the most extreme seasonal tropical forest climates with high maximum temperatures and high seasonal water deficits. This means that some Amazonian forests are already at the climatic limits capable of sustaining productive tropical forest ecosystems. Further heating or drying in the Amazon risks pushing its trees beyond critical physiological thresholds.

4.5. Recommendations

- Document ecological networks and their implications for maintaining these ecosystems in the long-term to understand the truly astounding ecological and evolutionary relationships among species and ecosystems.
- Conservation initiatives must protect not only forests, but also all the animal and plant species within them to guarantee ecological functioning. Large individual areas of forests, savannas, and aquatic ecosystems need to be protected to establish large-scale, landscape-level conservation initiatives, maintain core areas, and provide security for the survival of wide-ranging species, migratory species, innumerable less abundant species, species with patchy distributions, and the full range of functional traits.
- Maintain connectivity of ecosystems and landscapes from the Andes to the Amazon region, as well as the interaction between terrestrial and aquatic environments. This is vital to ensure that Amazonian diversity and processes can be sustained.
- Ensure large, connected areas spanning climate gradients are protected. Connecting Amazonian and Andean forests is especially essential for ensuring that forest functions are maintained in a changing climate, and that Amazonian species have some prospect of being able to track climate change in space.

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Chapter 5

The Physical hydroclimate system of the Amazon

Vista aérea da Terra Indígena Yanomami (Foto: Bruno Kelly/Amazônia Real)

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Graphical Abstract

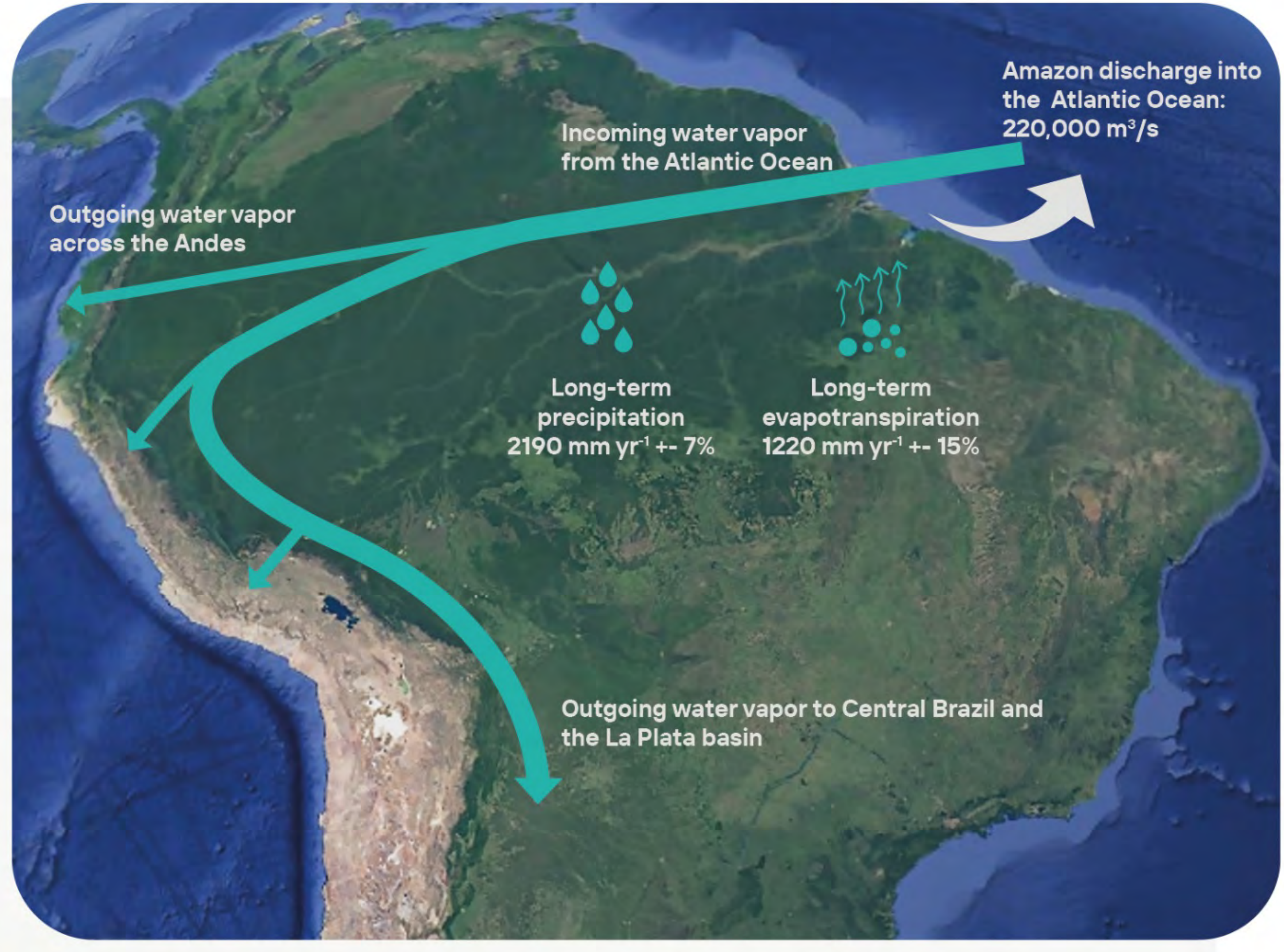

Figure 5.. Graphical Abstract

The physical hydroclimate system of the Amazon

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Key Messages

- Given its tropical location enclosed by the Andes, its huge spatial extent (7.3 million km^2, including the Tocantins), and forest cover, the Amazon River Basin is one of the most critical elements of the Earth's climate system. It is the largest and most intense land-based convective center, exerting a strong influence on atmospheric dynamics and circulation patterns both within and outside the tropics. It produces rainfall that results in the largest river discharges on Earth at 220,000 m^3/s, corresponding to 16-22% of the total world river discharge.
- The Amazon Basin is mainly characterized by lowlands with a warm and rainy climate. The upper part of the basin includes the eastern slope of the Andes, characterized by a wide variety of mountain climates (cloud forest, Páramos, Yungas, Punas, etc.).
- The El Niño-Southern Oscillation (ENSO) is the main cause of interannual variability in rainfall. ENSO is typically (but not exclusively) accompanied by droughts in the Amazon region, with recent severe droughts producing low river water levels, a high risk of forest fires, and impacts on natural river ecosystems. In addition to ENSO, Atlantic and Pacific SST variability influence the climate of the Amazon at interannual and interdecadal time-scales, including extreme events.
- In the last 15 years, the Amazon has witnessed several climate extremes: droughts in 2005, 2010, and 2015–16 and floods in 2009, 2013, 2014, and 2017, and 2021. Some of these have been classified as "once-in-a-century" events. Historical records show previous droughts in 1926, 1964, 1980, 1983, and 1998 and floods in 1953, 1988, and 1989.

Abstract

The physical hydroclimate system of the Amazon operates on several spatial and temporal scales. Large-scale processes, including solar forcing, control the main seasonal patterns of atmospheric circulation, rainfall, river discharge, and flooding. For example, persistent patterns of sea surface temperature, such as those associated with the El Nino/Southern Oscillation, are associated with the main modes of interannual and interdecadal climate variability. Mesoscale processes such as those related to topography or land-atmosphere interactions cause other localized circulations. While the ultimate source of water in the basin is evaporation from the oceans, this water is recycled through evaporation and reprecipitation before being exported back to the ocean through the flow of the Amazon River or exported in the form of water vapor from the basin. The abundant rainfall in the Amazon Basin (averaging 2,190 mm per year) is thus a consequence of intense radiative heating, low-level convergence of oceanic water vapor, and permanent re-injection of water vapor into the atmosphere by the rainforest itself, aided by the mechanical

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uplifting of air by the Andes. Land surface processes partition precipitation into evapotranspiration (~1,220 mm per year), surface runoff, and deep drainage to the groundwater. The Amazon River system drains the surface and groundwater components of this abundant rainfall, forming the world's largest watershed and feeding the world's largest river, with a mean discharge of 220,000 m^3/s. The Amazon has a discharge five times larger than the Congo, the world's second-largest river. The flow is highly seasonal, and imbalances between the addition of water to rivers by rainfall and the rate of water export downstream cause seasonal flooding over a large floodplain area, with beneficial ecological and biogeochemical implications. Extreme flood and drought events are associated with intense interannual rainfall variability, which, in turn, influence forest fires and biogeochemical cycles.

Keywords: Amazon water balance, extreme events

5.1 Introduction

The Amazon is one of the three permanent centers of convection in the intertropical zone (along with Central Africa and Southeast Asia) – i.e., one of the main centers of ascending air that transports energy from land to the atmosphere. It is also the most powerful of these three land-based convective centers, exerting strong influences on atmospheric circulation both within and outside the tropics. As one of the main drivers of the Hadley-Walker circulations, the Amazon is a critical energy source to the atmosphere, removing latent heat from the surface by evaporation and transpiration of water (a process termed evapotranspiration), and releasing that heat to the atmosphere when water condenses and forms clouds or precipitation. The strength of the Amazon convective center is mainly due to its geographical characteristics, including its large size, position spanning the equator, and the presence of the Andes mountains located downwind in the basin. As explained throughout this chapter, the rainforest also contributes to strengthening this convective center. The low albedo of the rainforest increases the absorbed net radiation, and the constant flux of water vapor to the atmosphere from the rainforest via evapotranspiration adds energy to the mean convection fields. At the same time, it smooths seasonal and interannual variability of convection and rainfall in the region.

The region's abundant convection and rainfall, along with the basin's large size, produce the world's largest river, flanked by a complex network of channels and floodplains that transport sediments, carbon, and other nutrients. Intense seasonality and interannual variability of the water cycle are also dominant factors for local riverine communities who may have their towns either flooded or completely isolated depending on the status of this river system – dictated by the modes of interannual climate variability of rainfall (Marengo and Espinoza, 2016).

Table 1 presents a synthesis of several estimates of the Amazon River Basin's long-term water balance. Long-term estimates of precipitation (P) show little variability across studies, with a median value of ~2190 mm/yr±7%.

The long-term mean runoff (R) is estimated at 1100 mm/yr±15%, which yields a median runoff coefficient (C=R/P) of 0.51±0.08.

Estimates of evapotranspiration (ET) have much higher uncertainties by comparison, with median values of ~1250 mm/yr±50%. This imbalance is likely because most high estimates of ET (>1500 mm/yr) are derived from reanalysis data, which (by design) do not conserve mass over the long-term. If these high values are excluded, the median value of ET is closer to 1220 mm/yr±15%, with a median evaporative fraction (EF = ET/P) of 0.54±0.07. Over the long term the total rainfall must be partitioned either into runoff or evaporation. Table 1 shows estimates of this balance made in the literature – with many estimates splitting precipitation evenly between ET and runoff.

Table 5.1. Long-term water balance of the Amazon river basin according to several studies. Studies marked by an asterisk (*) include the Tocantins river basin. Precipitation (P), evapotranspiration (ET), runoff (R), and the imbalance (P – ET – R) are expressed in mm/yr. The runoff coefficient (C = R/P) and evaporative fraction (EF=ET/P) are dimensionless variables.

Studies	**Period**	**P**	**R**	**ET**	**C** **(R/P)**	**EF** **(ET/P)**	**Imbalance** **P-E-R**
Costa and Foley (1999)*	1976-1996	2160	1106	1679	0.51	0.78	-625
Zeng (1999)	1985-1993	2044	1095	1879	0.54	0.92	-930
Salazar (2004)	1961-1990	2189	940	1248	0.43	0.57	1
Marengo (2004)*	1970-1999	2117	1059	1570	0.5	0.74	-512
Getirana *et al.* (2014)	1989-2008	2208	1188	1033	0.54	0.47	-13
Carmona (2015)	1982-2008	2266	1163	1189	0.51	0.52	-86
Builes-Jaramillo and Poveda (2018)	1984-2007	2225	965	1248	0.43	0.56	12

This chapter reviews the main features and the main large-scale and mesoscale mechanisms that cause the mean Amazon climate, its interannual and interdecadal variability, and extreme drought and flood events (Sections 5.2 and 5.3). The effects of extreme events on vegetation dynamics are discussed in Section 5.3. Next, the chapter describes the partitioning of precipitation into evapotranspiration (Section 5.4), runoff, flow seasonality, and floodplain dynamics (Section 5.5). Finally, the role of floodplains in biogeochemical cycles is discussed in Section 5.6.

This chapter's description of the Amazon's physical hydroclimate system also serves as an introduction to the biosphere-atmosphere interactions discussed in Chapters 6 and 7, and to climate change as discussed in Chapter 22. Chapter 6 discusses the influence of the physical hydroclimate system on biogeochemical cycles, whereas Chapter 7 presents the rainforest's role in the water and energy exchange of this coupled biosphere-atmosphere system. Chapter 22 presents the long-term variability and changes in temperature and hydrometeorology in the Amazon.

5.2 Main features of the Amazon climate

5.2.1 Spatial distribution of climate variables

5.2.1.1 Air temperature Due to high, relatively constant incoming solar radiation, air temperature in the Amazon is practically isothermal, with only a small variation throughout the year except in the southern part (Rondônia, Mato Grosso, Bolivian Amazon, and the Southern Peruvian Amazon). Annual averages show very high temperatures in the central equatorial region, exceeding 27-29ºC. The seasonal thermal amplitude is 1-2ºC, and average values range from 24°C to 26ºC. The city of Belém (PA) has a maximum monthly average temperature of 26.5ºC in November, and a minimum of 25.4ºC in March, while Manaus (AM) has its temperature extremes in September (27.9ºC) and April (25.8ºC). In austral winter, the cold air masses that produce frosts in the South and Southeast of Brazil can also cool the southern and western Amazon, with significant air temperature drops (Ricarte and Herdies 2014, Viana and Herdies 2018). Near the Andes, the maximum monthly mean temperature in Santa Cruz de la Sierra, Bolivia, reaches 26.1°C in September and 20°C in June. Despite small seasonal fluctuations, large temperature oscillations (high amplitude) are typical of the diurnal cycle in this region, in association with the timing of local rainfall.

5.2.1.2 Atmospheric circulation The mean atmospheric circulation in the Amazon is forced by the annual cycle of solar radiation. The atmospheric circulation's main features are described here, while the solar forcing is described in Section 5.3.2. Near the Amazon delta, maximum rainfall is observed during austral summer-fall, and dry conditions prevail during wintertime (Figure 5.1). This is due to the alternating warming of the two hemispheres and to the annual cycle associated with the seasonal meridional migration of the Intertropical Convergence Zone (ITCZ) (Vera *et al.* 2006a). The trade winds coming from the tropical North and South Atlantic converge along the ITCZ and are associated with subtropical anticyclones in the North and South Atlantic.

Monsoonal rain over the Amazon Basin during austral summer provides moisture to establish an active South Atlantic Convergence Zone (SACZ; Figure 5.1). The SACZ is characterized by a convective band that extends northwest-southeast from the Amazon Basin to the subtropical South Atlantic Ocean. It is identifiable by persistent cloudiness and frequently configured in the austral summertime (Ambrizzi and Ferraz 2015). The SACZ´s northern edge merges with the Atlantic ITCZ (Cai *et al.* 2020). Diabatic heating in the Amazon Basin con-

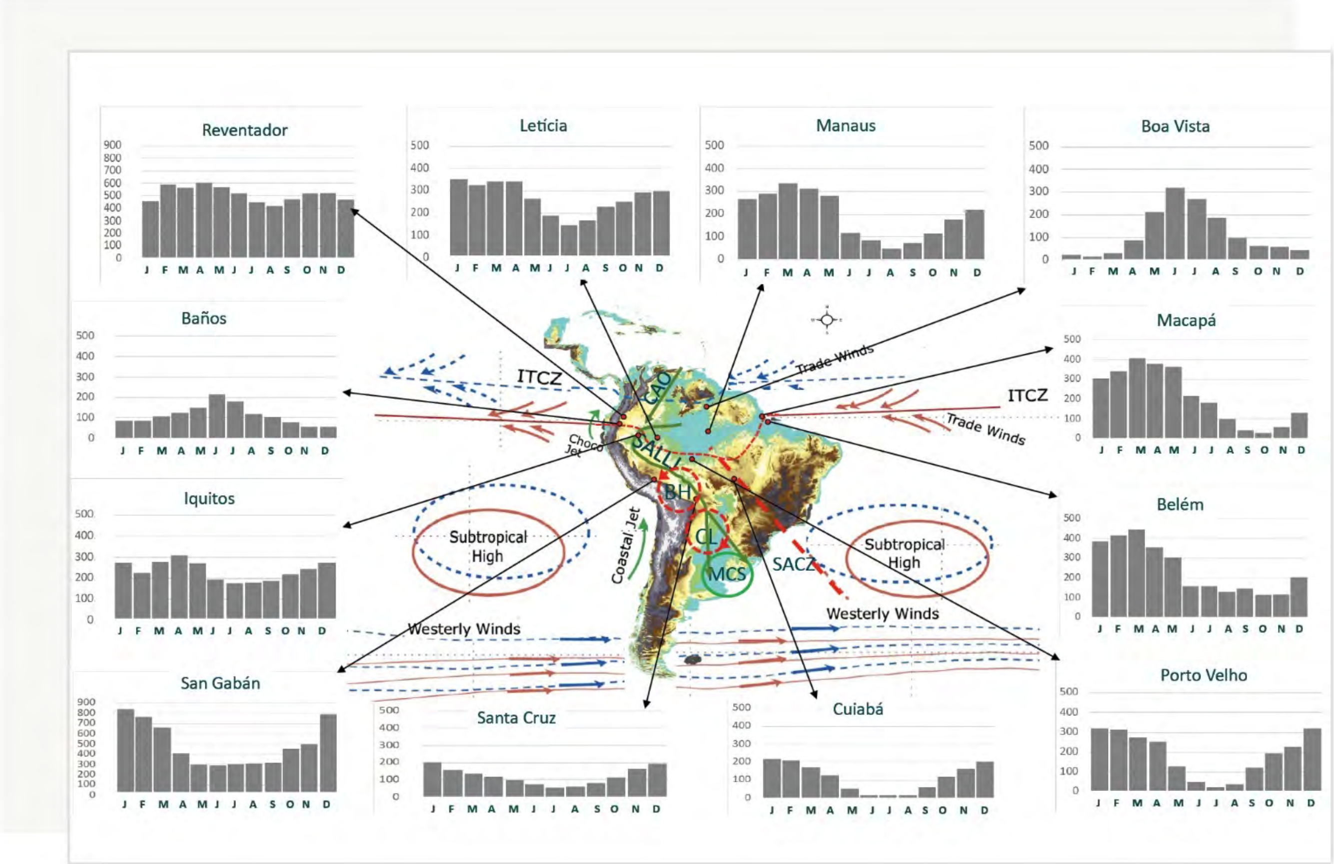


Figure 5.1 Schematic of the main climatological features in South America. The blue and red lines represent June-July-August (JJA) and December-January-February (DJF), respectively. The annual cycle of rainfall (bars) is shown for stations located in various sections of the Amazon region (in mm), indicated by dots. Low-level circulation features: CL, Chaco Low; BH, Bolivian High; ITCZ, Intertropical Convergence Zone; MCS, mesoscale convective system; SACZ, South Atlantic Convergence Zone; SALLJ, South American low- level jet. Sources of rainfall data: INMET and ANA (Brazil), SENAMHI (Peru), SENAMHI (Bolivia) and INAMHI (Ecuador). The figure is adapted from Figure 1 of Cai *et al.* (2020). Climatology is for the period 1961-2010.

tributes to the formation of the Bolivian High (BH) in the upper atmosphere (Lenters and Cook 1997). At the regional scale, moisture transport in and out of the Amazon Basin is critical for the rainfall regime, particularly during the wet season. The moisture from the Amazon is exported out of the region, transported via the South American Low-Level Jet (SALLJ) east of the Andes, interacting with the Chaco Low (CL) and contributing to precipitation over the La Plata Basin by intensifying mesoscale convective systems (Marengo *et al.* 2004, Drumond *et al.* 2008, 2014; Arraut *et al.* 2012; Vera *et al.* 2006b, Liebmann and Mechoso 2011, Jones and Carvalho 2018, Gimeno *et al.* 2016, 2020, Jones 2019, Cai *et al.* 2020).

5.2.1.3 Rainfall Because it extends into both hemispheres, the Amazon is characterized by several rainfall regimes due to the alternating warming of each hemisphere. During a 'normal' year, rainfall in the region shows opposing phases between the northern and southern tropics, with a rainy season in austral winter in the north and austral summer in the south. In the southern Amazon, rainfall peaks during austral summer; in the central Amazon and near the Amazon delta, it peaks in austral autumn; and north of the Equator, it peaks in austral winter (Figure 5.1). The northwest equatorial region experiences low rainfall seasonality, with wet conditions throughout the year. For more details about rainfall regimes in the Amazon Basin, see Figueroa and Nobre (1990), Rao and Hada (1990), Rao *et al.* (2016), Espinoza *et al.* (2009a, 2015), Debortoli *et al.* (2015), Marengo and Espinoza (2016), and Cai *et al.* (2020).

The onset and demise of the rainy season in the Amazon varies gradually from south to north. The end of the rainy season is more regular than its onset. The rainy season in the southern Amazon ends in April, while in the north it ends in September. SST anomalies in the Pacific or Tropical Atlantic play a dynamic role in controlling the beginning and end of the rainy season (Liebmann and Marengo 2001, Liebmann *et al.* 2007; Arias *et al.* 2015).

5.2.2 The role of ENSO and other large-scale mechanisms

5.2.1.1 ENSO The El Niño-Southern Oscillation (ENSO) is the main cause of global interannual variability in the water and energy budgets. ENSO extremes represent a reversal of the typical SST patterns in the Tropical Pacific – El Niño (EN)/La Niña (LN), when there is warming/cooling in the eastern or central-eastern tropical Pacific. EN is typically (but not exclusively) accompanied by drought in the Amazon region. In general, recent severe droughts over the Amazon have resulted in low river water levels, a high risk of forest fires, and impacts on natural river ecosystems (Cai *et al.* 2020).

Changes to atmospheric circulation during EN and drought have been summarized by Builes-Jaramillo *et al.* (2018a) and Jiménez-Muñoz *et al.* (2019). Observed anomalies in the vertical distribution of zonal and meridional wind are consistent with SST anomalies. During drought and EN years, subsidence anomalies appear over areas with negative rainfall differences over the Amazon, with convection and intense rainfall over warm SST in the eastern Equatorial Pacific region. The upper-level convergence anomalies observed during drought years over tropical equatorial South America (east of the Andes) are consistent with low-level subsidence anomalies. This suggests anomalies in the upper and lower branches of the Hadley circulation over tropical South America east of the Andes, and of the Walker circulation over the equatorial Atlantic. The ascending branch of the Walker circulation over the eastern central Pacific is the main driver of the subsidence branch over the Amazon Basin east of the Andes, which extends all the way to the tropical Atlantic.

There are different "types" of EN depending on the location of maximum warm anomalies over the tropical Pacific, Eastern Pacific (EP) EN or Central Pacific (CP) EN (Takahashi *et al.* 2011). Because the Hadley and Walker circulations are affected differently during EP-EN and CP-EN episodes (Zheleznova and Gushchina 2017), they lead to different precipitation anomalies over South America

(Tedeschi and Collins 2017; Sulca *et al.* 2018). Physical mechanisms behind the different patterns of rainfall deficits during CP- and EP-ENs and warm Tropical Northern Atlantic Index (TNA) events are described in Jiménez-Muñoz *et al.* (2019). EP-EN years were detected in 1983 and 1998, whereas CP-EN occurred in 2010 and 2016 (Sulca *et al.* 2018; Gu and Adler 2019, Gloor *et al.* 2013, 2018).

5.2.2.2 PDO, AMO, MJO In addition to ENSO, there are two other modes of interannual and interdecadal variability with teleconnections that influence the climate of the Amazon, The Pacific Decadal Oscillation (PDO) and the Atlantic Multidecadal Oscillation (AMO). They represent changes in the organization of air-sea interactions that vary at decadal scales and affect the sea surface, inducing later circulation and rainfall changes in the Amazon. For a detailed definition of these modes of variability, please see the Glossary.

Consistent with the ENSO (EN) positive phase, the PDO and AMO's positive phases matched the intensification of negative rainfall anomalies in the Amazon towards the end of 2015, during the 2015-16 EN event (Aragão *et al.* 2018). This finding is consistent with previous work (Kayano and Capistrano, 2014) showing that the Atlantic Multidecadal Oscillation (AMO) and ENSO influence South American rainfall at the end of the year, before the peak of EN.

Positive phases of the PDO are associated with an increase in precipitation in the central and northern parts of the basin and a decrease in the southern regions (Gloor *et al.* 2013). Andreoli and Kayano (2005) show that EN effects on rainfall over South America differ from those of the PDO phases in the Amazon. For example, they show negative precipitation anomalies for the warm PDO regime, consistent with the descending motion and cyclonic circulation over northern South America and the adjacent Atlantic sector. On the other hand, the relatively weaker circulation patterns in these sectors result in smaller magnitude precipitation anomalies in the Amazon for the cold PDO phase.

The intraseasonal variability is particularly important during the austral winter (Mayta *et al.* 2018). Previously, Souza and Ambrizzi (2006) found that the Madden–Julian Oscillation (MJO) is the main atmospheric mechanism influencing rainfall variability at intraseasonal timescales over the eastern Amazon and during the rainy season in northeast Brazil. During the drought of 2005, however, the intraseasonal oscillation was weaker than normal, favoring drought conditions in the region. The Tropical North Atlantic played a major role in this drought (Builes-Jaramillo *et al.*, 2018b).

5.2.3. Extreme drought and flood events

In the last 15 years, the Amazon Basin has witnessed climate extremes, some of them characterized as 'events of the century'; droughts in 2005, 2010, and 2015–16; and floods in 2009, 2012, 2014, and 2021. Historical records show previous droughts in 1926, 1964, 1980, 1983, and 1998; and floods in 1953, 1988, 1989, and 1999. These events have been linked to modes of natural climate variability (EN, warm TNA anomalies) with strong impacts on natural and human systems. Some of the Amazon's main cities were flooded during flood years or isolated by extremely low river levels during droughts. The number of fires increased during drought years, releasing carbon, smoke, and soot into the atmosphere and affecting the local population (Marengo and Espinoza 2016, Gatti *et al.* 2014, Aragão *et al.* 2018, Jiménez-Muñoz *et al.* 2016, 2019). The year 1999 and other wet years (1988-89, 2007-2008, and 2011-2012) were LN years (see Chapter 22). It is worth mentioning that droughts and floods are not synchronous and do not affect the whole basin in the same way, as seen in Figures 5.2 and 5.3.

Overall, droughts affect the north-central Amazon, but the spatial pattern differs from one EN event to another and even from one drought case to another (Figure 5.2). Droughts in the Amazon have been related to EN events, such as in 1912, 1926, 1983, 1997–1998, and 2015-16 (e.g., Aceituno 1988; Williams *et al.* 2005, Coelho *et al.* 2013, Marengo *et al.* 2018, Jiménez-Muñoz *et al.* 2018, 2019). However, the 1964 and 2005 severe droughts were exceptions, indicating TNA's active influence on those extremes (Marengo *et al.* 2008, Zeng *et al.*, 2008, Builes-Jaramillo *et al.*, 2018b). The 2010 extreme drought was related to the successive occurrences of an El Niño in austral summer and a very warm TNA in the boreal spring and summer (Espinoza *et al.* 2011; Marengo *et al.* 2011, Lewis *et al.* 2011, Gatti *et al.* 2014, Andreoli *et al.* 2012). Figures 5.2 and 5.3 show seasonal rainfall anomalies in South America for drought and wet years, respectively. In each case, whether EN or not, the geographical distribution of droughts may differ, affecting the southeastern, central, or northern Amazon differentially, and thus impacting the region's hydrology.

5.2.4 Andean-Amazon hydrometeorology and variability

This section focuses on the western Amazon, including the Andean part of the Amazon Basin. The region encompasses the upper Madeira Basin in Bolivia, Peru, and Brazil; the Amazonas-Solimões Basin in Peru and Ecuador; and the Japurá-Caquetá Basin in Colombia and Brazil. This region presents a wide variety of mountain climates, including humid conditions in the cloud forests, Páramos, and Yungas, and dry conditions in the highland Punas.

5.2.4.1 Seasonal patterns Seasonal rainfall cycles in the upper part of the Andean-Amazon Basins of Colombia and Ecuador follow a unimodal regime with a wet season during the boreal summer (Laraque *et al.* 2007; Arias *et al.* 2020). In these basins, river discharge peaks around May-July (e.g., Napo and Caquetá rivers in Figure 5.7), a pattern associated with the intensification of westward moisture advection from the equatorial Amazon Basin and orographic uplift forced by the Andean topography during boreal summer (Rollenbeck and Bendix 2011; Campozano *et al.* 2016).

The Andean-Amazon Basins of Ecuador exhibit a bimodal annual cycle of precipitation, with peak discharge observed around March-April and October-November in the upper part of the Napo, Pastaza, and Santiago Basins (Campozano *et al.* 2018) (e.g., Reventador station in Figure 5.1). Consequently, the lowlands of these intra-Andean Basins follow a bimodal annual cycle of discharge with peaks around June-July and October-November (Laraque *et al.* 2007). In these regions, less rainfall during boreal summer is associated with atmospheric subsidence that inhibits convective activity (Campozano *et al.* 2016; Segura *et al.* 2019).

In the southern tropical Andean-Amazon Basins (mainly south of 8°S), the dry season occurs in June-August and the rainy season in December-March, linked to the mature phase of the South American Monsoon System (SAMS) and the meridional movement of the ITCZ. River discharges over these basins show unimodal cycles peaking around January and March (e.g., Beni, Ucayali and Huallaga rivers in Figure 5.7; and Santa Cruz and San Gabán stations in Figure 5.1) (Espinoza *et al.* 2011; Lavado-Casimiro *et al.* 2012; Molina-Carpio *et al.* 2017). Rainfall seasonality is particularly strong in the upper and drier part of the Andean-Amazon Basins (usually above 3,000 m), where around 75% of total annual rainfall is observed between November and March (~100 mm/month), driven by upward moisture transport from the Amazon toward the mountains (Garreaud *et al.* 2009). Easterly winds in the upper troposphere (200-300 hPa) also favor moisture fluxes from the Amazon to the Andes at different time scales (Garreaud *et al.* 2009; Segura *et al.* 2020).

Most of the Amazon’s Andean tributaries drain to two main rivers, the upper Madeira river (mainly from the Bolivian and southern Peruvian Amazon) and the Amazonas-Solimões river (mostly from the Peruvian and Ecuadorian Amazon) (Figure 5.7). At the Porto Velho station, the basin of the upper Madeira river spans 975,500 km^2, of which 23% are in the Andes. Mean annual discharge at Porto Velho is estimated at 18,300 m^3/s, with peak values around 36,000 m^3/s from March-April and lows around 5,000 m^3/s from September-October (Molina-Carpio *et al.* 2017) (Figure 5.7). At the Tabatinga sta-

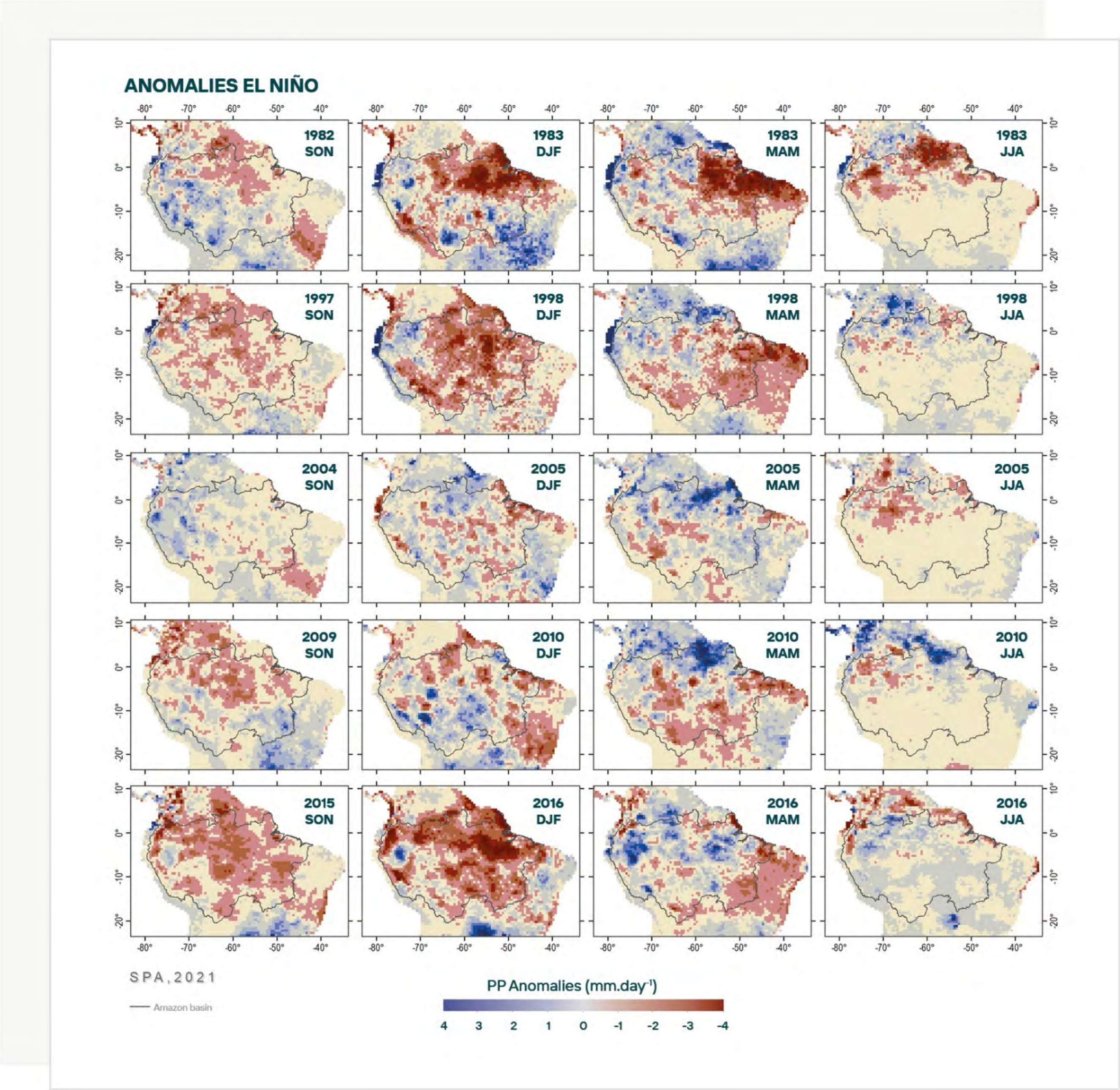


Figure 5.2 Spatial patterns of precipitation anomalies during seasons DJF, MAM, JJA, and SON for drought years in the Amazon. These are for different strong EN and TNA warming. Precipitation anomalies were obtained from the CHIRPSv2.0 dataset using the reference period 1981-2010. A black contour marks the Amazon Basin. Adapted from Jiménez-Muñoz et al. (2021; ©RMetS).

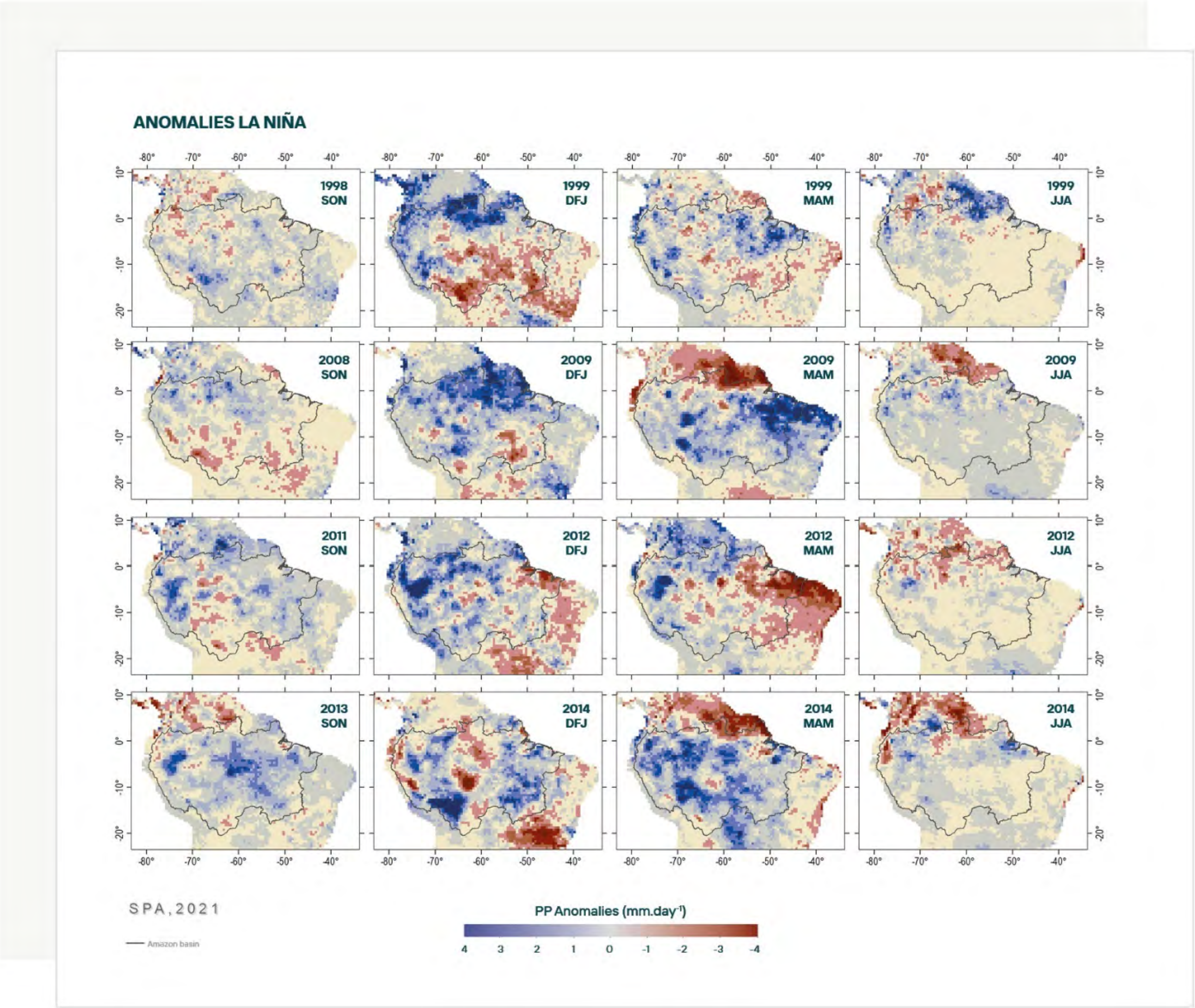


Figure 5.3. Same as in Figure 5.2 but for wet episodes (2019; ©RMetS).

tion, the Amazonas-Solimões river Basin spans 890,300 km^2, of which ~40% are in the Andes. The mean annual discharge at Tabatinga is estimated at 38,000 m^3/s, with peak values around 51,000 m^3/s from April-May and lows around 20,000 m^3/s in September (Lavado-Casimiro *et al.* 2012) (Figure 5.7).

5.2.4.2 Interannual variability and extremes In the Andean-Amazon region, a rainfall deficit (excess) during austral summer is frequently associated with El Niño (La Niña) events (Poveda *et al.* 2006; Espinoza *et al.* 2011). However, different patterns occur in the upper and lower parts of the Andean-Amazon Basins (Arango-Rueda and Poveda 2019). Recent studies have also reported different precipitation anomalies for the Central-Pacific and Eastern-Pacific El Niño types (Lavado-Casimiro and Espinoza 2014; Sulca *et al.* 2018; Navarro-Monterroza 2019). In general, the Central-Pacific El Niño (La Niña) is associated with rainfall deficits (excesses) in the upper part of the basin (the Andean regions of Colombia, Ecuador, and Peru). These anomalies are weaker during Eastern-Pacific El Niño (La Niña) events. In contrast, in the upper Madeira Basin rainfall anomalies are stronger during the Eastern-Pacific El Niño.

On seasonal timescales, rainfall anomalies over the Andean Amazon Basin range from ±0.5 to ±2.0 mm/day and can persist over periods of several months (Sulca *et al.*, 2018; Jiménez-Muñoz *et al.*, 2021). During the austral autumn, winter, and spring, rainfall anomalies over the Andean-Amazon region are mainly related to SST variability in the TNA, which is the main source of atmospheric moisture for the Andean-Amazon region (Arias *et al.* 2015; Hoyos *et al.* 2017; Poveda *et al.* 2020). Warm TNA anomalies are associated with increased precipitation in Colombia and Venezuela, related to enhanced atmospheric water vapor transport from the tropical Atlantic and the Caribbean Sea toward northern South America (e.g., Arias *et al.* 2020). In the Andean-Amazon regions of Ecuador, Peru, and Bolivia, warm conditions in the TNA are related to rainfall deficits, associated with a reduction in moisture advection from the Atlantic Ocean and enhanced atmospheric subsidence over the central and southern Amazon (Silva *et al.* 2008, Espinoza *et al.* 2019a; Jiménez-Muñoz *et al.* 2021).

As a result of rainfall anomalies, extreme hydrological events in the Andean-Amazon Basins have been associated either with El Niño/La Niña events or with SST anomalies in the TNA. The very unusual wet austral summer period of 2014, originating on the eastern slopes of the Peruvian and Bolivian Andes, was associated with warm anomalies in the western Pacific-Indian Ocean and over the subtropical South Atlantic Ocean (Espinoza *et al.* 2014). Wet conditions in the Bolivian Amazon during the 2014 austral summer were superimposed on flood waves from the main sub-basins, producing major floods in the region that same year (Ovando *et al.* 2016). This was also related to long-term atmospheric blocking systems during January and February of 2014 over southeastern Brazil, which ultimately caused the drought over São Paulo during the austral summer of 2014. In the higher part of the Amazon Basins' inter-Andean rivers, floods are frequently triggered by intense storms and/or rapid glacier melting during the austral spring-summer (Huggel *et al.* 2015).

5.3 The Amazon convection and mesoscale circulations

5.3.1 Nature of the Amazon convection

Atmospheric deep convection is typical in the tropics in association with the ascending branch of the Hadley-Walker cells. Upward motion extends from near the surface to above the 500 hPa level, reaching the level of free convection (LFC) where buoyant convection begins. At the large-scale (>1,000 km), seasonal changes in the thermal contrast between tropical South America and the Atlantic Ocean modulate wind circulation, which supplies the available energy and moist instability over the Amazon Basin (Vera *et al.* 2006a). These features provide the convective available potential energy (CAPE), gross moist instability, and rising motion essential to produce deep atmospheric convection (Garstang *et al.* 1994; Cohen *et al.* 1995; Zhou and Lau 1998). At regional (100-1,000 km) to local scales (<100 km), Amazon convection is also related to the land surface wet-bulb temperature, generally above 22°C (Eltahir and Pal 1996), which is closely determined by surface humidity and sensible and latent heat fluxes from the local land surface (Fu *et al.* 1999).

Deep atmospheric convection contributes about 80% of the total annual precipitation in the Amazon Basin, while only 20% of yearly rainfall is associated with local systems (Greco *et al.* 1990). Seasonal changes in convection are related to changes in the moistening of the planetary boundary layer (PBL) and changes in the temperature at the top of the PBL (Fu *et al.* 1999; Liebmann and Marengo 2001). However, in the northwestern Amazon, deep convection is particularly intense year-round because the warmer land surface provides a highly unstable atmospheric profile. In addition, the concave shape of the Andes induces a low-level convergence over the northwestern Amazon Basin, which is related to high annual rainfall (>3,000 mm) in this region (Figueroa and Nobre 1990; Espinoza *et al.* 2009b). Because deep convection over the Amazon is related to a strong release of latent heat, the Amazon basin is an important source of energy. Through the equatorial Kelvin and Rossby waves and their interactions with the orography, the Amazon modulates the main regional structures of the atmospheric circulation in South America (Silva Dias *et al.* 1983; Figueroa *et al.* 1995; Junquas *et al.* 2015).

5.3.2 Solar forcing

Following the seasonal migration of the solar radiation maximum, the major heating zone migrates from northernmost South America (including the northern Amazon Basin) in austral winter to the central and southern Amazon in austral summer (Horel *et al.* 1989). Consequently, convective activity and rainfall enhancement show a seasonal displacement following the heating zone migration (see Section 5.2.1). Figure 5.4 shows the spatial and temporal evolution of the outgoing longwave radiation (OLR) in tropical South America, closely related to solar forcing and the development of deep convection.

The alternating warming of the two hemispheres modulates the seasonal displacement of the ITCZ, including its Amazonian part (Figure 5.1) and the ascendant branch of the Hadley-Walker cells, which is associated with maximum rainfall over the equatorial Amazon Basin. Over this region, solar radiation peaks at the equinoxes (Figure 5.4), and the northeastern Amazon Basin displays the maximum precipitation in the austral autumn, with peaks in April and May. However, in some western equatorial Amazon regions, the wet season occurs during austral fall and spring (see Section 5.2.1). In austral spring, surface heating by solar radiation is highest over the central and southern Amazon (south of 5°S), where deep convection appears. By late November, deep convection happens over most of the Amazon Basin, mainly from 5°S to 20°S, but it is still absent over the eastern Amazon Basin and northeast Brazil (Horel *et al.* 1989; Zhou and Lau 1998).

At the peak of austral summer, following the southward migration of the sun, heating and convective activity moves toward the subtropical highlands. Rainfall peaks over the central Andes and the southern Amazon Basin during this season. The thermal contrast between the continent determin-

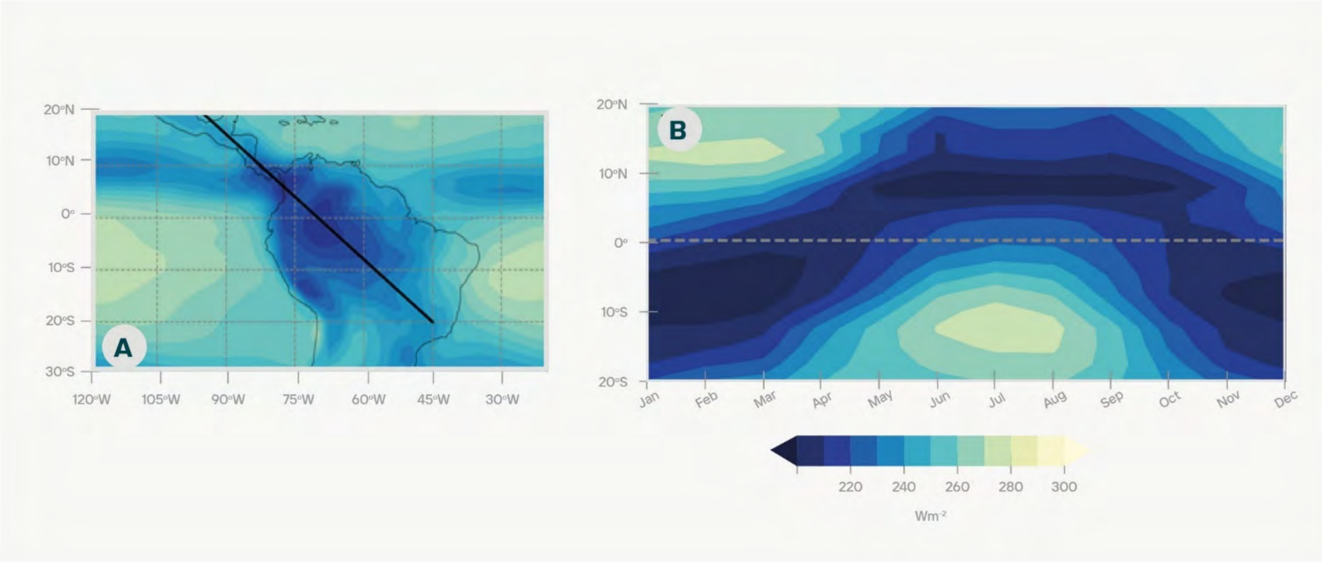


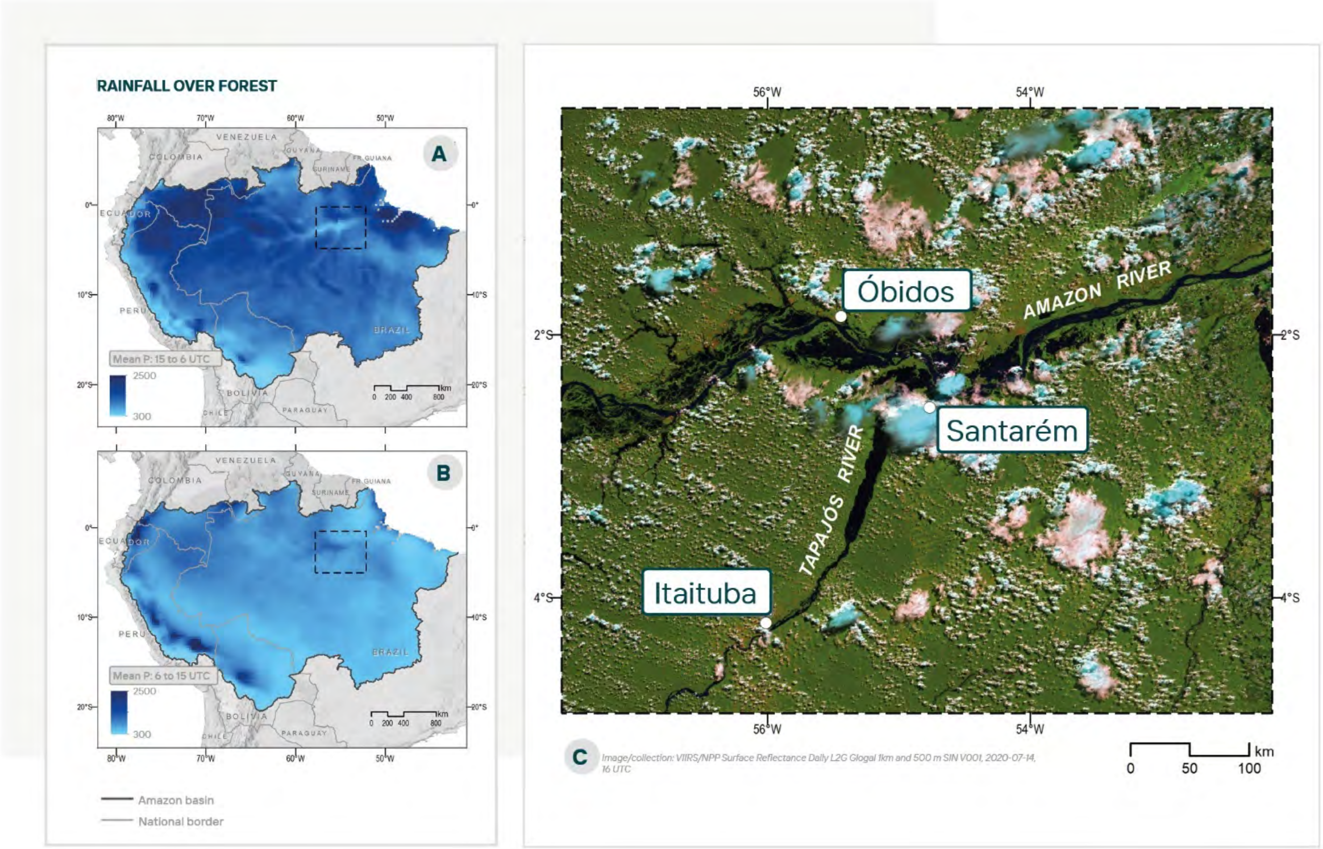
Figure 5.4 (A) 1974-2019 mean annual values of outgoing longwave radiation (OLR, in W.m^{-2}) over tropical South America. (B) Time-latitude diagram of the climatology of monthly OLR (1974-2019) averaged across a 10° longitudinal strip centered on the black line over tropical South America shown in (a). Adapted from Horel *et al.* (1989). Interpolated OLR data provided by the NOAA/OAR/ESRL PSL (HTTPS://PSL.NOAA.GOV; Liebman and Smith 1996).

es the SAMS configuration (Marengo *et al.* 2012). The mature phase of the SAMS (typically from late November to late February) exhibits four dominant features (Section 5.2.1 and Figure 5.1): (i) an anticyclone located over Bolivia at 200–300 hPa (the Bolivian High -BH); (ii) the occurrence of high surface temperatures over the Atlantic Ocean before the wet season begins in the southern Amazon; (iii) a northwest-southeast oriented band of maximum cloudiness over the southeast of the continent, the SACZ; and (iv) the intensification of the SALLJ to the east of the Andes (see review in Espinoza *et al.* 2020).

5.3.3 Forest breeze and river breeze circulations

Forest and river breezes are mesoscale (10-100 km) circulations close to large rivers. They result from differences in the sensible and latent heat fluxes between the hot land and the cool water during the daytime, which produces a horizontal pressure contrast. This mechanism enhances cloudiness over land during the day, while clear skies predominate over water. The opposite occurs during the night. In the Amazon Basin, convergence zones lead to enhanced rainfall over forests away from large rivers, and convective activity is reduced near rivers (e.g., Paiva *et al.* 2011; Figure 5.5).

Several studies have described river breezes in the central Amazon, using both observed and modeling approaches (e.g., Ribeiro and Adis 1984; Garstang and Fitzjarrald 1999; Cutrim *et al.* 2000). Near the Amazon-Tapajós confluence (Figure 5.5),



Image/collection: VIIRS/NPP Surface Reflectance Daily L2G Glogal 1km and 500 m SIN V001, 2020-07-14, 16 UTC

Figure 5.5 Rainfall estimated by TRMM 3B42 between (A) 15 to 06 UTC; and (B) 06 and 15 UTC. Adapted from Paiva *et al.* (2011). (c) Image of the VIIRS sensor (Visible/Infrared Imager Radiometer Suite) in true color corresponding to July 14 2020 at 16:48 UTC over the confluence of the Tapajós and Amazon rivers (dotted black box in a and b). By the NOAA/OAR/ESRL PSL (HTTPS://PSL.NOAA.GOV; Liebman and Smith 1996).

rain gauges close to large rivers show less convective rainfall in the afternoon. Still, this deficit is more than compensated by additional nocturnal rainfall (Fitzjarrald *et al.* 2008). Near Manaus, dos-Santos *et al.* (2014) show that river breezes and their impact on moisture transport are more evident during the dry season. The authors show that winds away from the rivers are frequent in the morning and afternoon, transporting moist air from the rivers to the city of Manaus. In contrast, winds blowing towards rivers are mainly observed at night.

River breezes affect moisture transport (Silva Dias *et al.* 2004) and local rainfall patterns. Paiva *et al.* (2011) showed a marked reduction in rainfall over the Solimões-Amazon river and along most Amazon tributaries. Since meteorological stations are often sited near large rivers (where most Amazon cities are situated), rain gauge-derived estimates of Amazon rainfall may be biased by river breezes (Silva Dias *et al.* 2004; Paiva *et al.* 2011).

5.3.4 Sea breeze and coastal circulations

The sea breeze system occurs at coastal locations due to the propagation of cool marine air towards inland areas. This system is initiated when the land surface heats faster than the sea surface (generally under relatively clear sky conditions). The thermal contrast creates a pressure gradient force directed from sea to land, causing a shallow layer of marine air to move inland (Miller *et al.* 2003).

Over the easternmost Amazon Basin, the presence of numerous bays, rivers, lakes, and the Atlantic Ocean create the ideal environment for the formation of local circulations, which modulate the regional weather and climate (Souza Filho 2005, Planchon *et al.* 2006; Germano and Oyama 2020). The main circulation patterns of the coastal and bay breezes over this region have been described elsewhere, based on observational and modeling studies (e.g., Silva Dias *et al.* 2004; Germano *et al.* 2017; Wanzeler 2018). In Belém (in the eastern Amazon Basin), the bay breeze starts in the morning and early afternoon. It is characterized by significant changes in wind direction from south to north (Matos and Cohen 2016) and is associated with the presence of stationary cloudiness. Rainfall peaks during the April-May season coincide with the sea breeze's maximum activity, which interacts with the Atlantic Ocean's trade winds to produce storm systems known as squall lines (Kousky 1980; Silva Dias 1987; Cohen *et al.* 1995).

Squall lines are multicellular storms that propagate inland in the Amazon Basin for over 1000 km at speeds of 50–60 km h^{-1} (Garstang *et al.* 1994; Greco *et al.* 1994). At the mesoscale, squall lines are characterized by advection of moisture produced by a sea breeze, a strong and deep low-level easterly jet, and a heat source in the central and western Amazon (Cohen *et al.* 1995). Strong jets tend to propagate the squall lines at higher speeds, with a longer lifetime and increased cloud development, forming thunderstorms with strong updrafts and downdrafts, as well as lightning. Downdrafts and lightning, in turn, cause disturbances that affect ecosystem dynamics, as described in Section 3.6.

5.3.5 Orographic-induced circulations and spatial rainfall distribution in the Andean-Amazon region

The Andean-Amazon hydrometeorology is characterized by interactions between regional atmospheric circulation, lowland-highland temperature contrast, and the complex Andean topography (e.g., Houze 2012; Roe 2005; Barry 2008). In addition, regional atmospheric circulation over South America is directly influenced by the Andean orography, particularly at low-levels (Figueroa *et al.* 1995). In the Andean-Amazon region, the SALLJ and the Llanos Jet (or *Corriente de los Andes Orientales*, CAO) are strongly controlled by the presence of the Andes, which acts like a barrier to the west, and the Amazon Basin to the east (e.g., Marengo *et al.* 2004; Jiménez-Sánchez *et al.* 2019). These LLJs are key elements of the South American atmospheric circulation because they transport vast quantities of moisture along large meridional distances throughout the east of the Andes. Indeed, the CAO's easterly flow reaches the eastern piedmont of the Andes as the northernmost leg of the SALLJ (Espinoza *et al.* 2020; Poveda *et al.* 2020).

At the local scale, Andean orography can influence atmospheric circulation through mechanical and thermal processes. The diurnal cycle of insolation generates thermally driven winds, such as anabatic (warm upslope) and katabatic (cold downslope) winds due to radiative warming of the surface during the day and radiative cooling during the late afternoon and night, respectively (e.g., Wallace and Hobbs 2006; Junquas *et al.* 2018). In addition, katabatic winds from the Andean highlands could trigger mesoscale convective systems (MCS) over the Andean-Amazon transition region (Trachte *et al.* 2010a,b; Kumar *et al.* 2020). Over this region, large and medium MCS are generally related to wet episodes, enhanced by the orographic lifting of moisture advection from the SALLJ (e.g., Giovannettone and Barros 2009; Romatschke and Houze 2013). Consequently, the mountainous precipitation diurnal cycle is associated with complex characteristics related to local atmospheric circulations (Poveda *et al.*, 2005; Junquas *et al.*, 2018). For example, on the eastern slopes of the tropical Andes, the highest precipitation rates are observed at night due to downslope wind and moisture transport (Figures 5.5a and b). Observational and modeling studies have shown that inter-Andean valleys also generate mechanical channelization of the moisture flux, which could contribute to moisture and rainfall over the tropical Andes, where glaciers, agriculture, and food security depend on precipitation. This includes regions such as La Paz, Cuzco, and the Mantaro valleys (Egger *et al.* 2005; Junquas *et al.* 2018; Saavedra *et al.* 2020). Convective activity forced by the Andes also generates sudden reversals of the river stage in the western Amazon (e.g., near Iquitos, Peru), where riparian agriculture is closely related to the annual hydrological cycle (Figueroa *et al.*, 2020).

Interactions between large-scale atmospheric circulation and the orographic circulations described above contribute to the high spatial variability of precipitation over the Andes-Amazon region. Studies have described a complex relationship between altitude and rainfall, which produces a strong spatial rainfall gradient associated with the windward or leeward exposure of the rain station to the dominant moist wind (Bookhagen and Strecker 2008; Espinoza *et al.* 2009b, Rollenbeck and Bendix 2011). The highest rainfall rates in the Amazon Basin (6,000–7,000 mm/year) are generally observed at about 400–2,000 m in the Amazon Basin of Colombia, Ecuador, Peru, and Bolivia (Poveda *et al.* 2014; Espinoza *et al.* 2015; Chavez and Takahashi 2017) (e.g., San Gabán station in Figure 5.1). As a result of these rainfall characteristics, the Andean Basins show the highest runoff per unit area of the Amazon River Basin (Moquet *et al.* 2011; Builes-Jaramillo and Poveda 2018), and Andean rivers drain sediments, pollutants, and nutrients downstream to the Amazon lowlands (McClain and Naiman 2008; Vauchel *et al.* 2017). In turn, the Amazon lowlands export water vapor and nutrients to the Andes through the moisture-laden trade winds, which is part of a strong interaction between the Amazon-Andes hydroclimatic system (e.g. Staal *et al.*, 2018; Weng *et al.*, 2018, Espinoza *et al.*, 2020).

5.3.6 The role of extreme weather events on ecosystem dynamics

At least two types of extreme weather events affect ecosystem dynamics and the natural carbon cycle. First, severe storms associated with squall lines can propagate strong downdrafts (Fujita 1990, 1981, Garstang *et al.* 1998) that cause forest blowdowns (Nelson 1994, Garstang *et al.* 1998, Negrón-Juárez *et al.* 2010, Espírito-Santo *et al.* 2010), affecting forest structure and species composition (Marra *et al.* 2014, Rifai *et al.* 2016, Magnabosco Marra *et al.* 2018, Chambers *et al.* 2009). Second, lightning is a frequent disturbance mechanism that can propagate fire and kill trees directly (Gora *et al.* 2020, Yanoviak *et al.* 2020, McDowell *et al.* 2018, Foster, Knight, and Franklin 1998). The frequency of lightning is positively associated with the density of large trees and biomass stocks in tropical forests (Gora *et al.* 2020). In the Amazon, this is important in the southern and eastern transition zones between forests and savannas, but also in Roraima state (Gora *et al.* 2020).

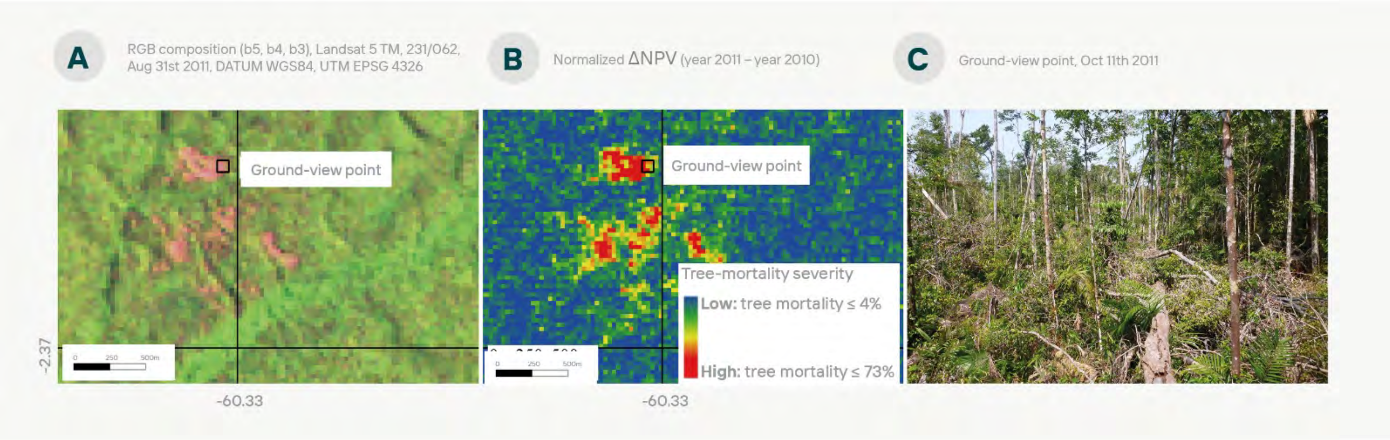


Figure 5.6 Forest blowdown (total area of ca. 91 ha) in 2011 in the Central Amazon, Brazil. Blowdowns can be identified on satellite imagery by geometric and spectral features such as defuse shape and high short-wave infrared reflectance, indicating non-photosynthetic vegetation (NPV) resulting from widespread tree damage and mortality (A). The severity of the associated tree-mortality can be estimated using normalized ΔNPV (year of the blowdown – previous year) combined with field-measured tree mortality (B). Edge of the blowdown/old-growth forest less than six months after disturbance, with toppled, survivor, and resprouting trees (C). By the NOAA/OAR/ESRL PSL (HTTPS://PSL.NOAA.GOV/; Liebman and Smith 1996).

5.3.6.1 Severe storms, blowdowns, and impacts on forest ecosystem dynamics Wind is a major cause of disturbance in forests worldwide, with impacts ranging from minor loss of leaves to widespread tree-mortality (Mitchell 2013). In the Amazon, convective storms can generate strong downdraft winds and extreme rainfall (e.g., 26-41 m s-1 and 30 mm h-1, respectively) (Garstang *et al.* 1998; Fujita *et al.* 1990; Negrón-Juárez *et al.* 2010) that can fell forest patches ranging in size from <2 ha (Negrón-Juárez *et al.* 2011) to >3,000 ha (Nelson *et al.* 1994). Large blowdowns can be associated with squall lines (Negrón-Juárez *et al.* 2010; Araujo *et al.* 2017). Forest blowdowns can be detected with remote sensing imagery because they create a large contrast in geometric and reflectance patterns between images acquired before and after the event (Figure 5.6A).

Blowdowns occur across the Amazon Basin, with the highest frequency in the Northwest region (Nelson *et al.* 1994; Negrón-Juárez *et al.* 2018; Espírito-Santo *et al.* 2010). In the Central Amazon near Manaus, blowdowns mostly occur during the transition from the dry to rainy season (Negrón-Juárez *et al.* 2017). The size distribution of blowdowns follows a power-law (Negrón-Juárez *et al.* 2018; Chambers *et al.* 2009), resulting in a mosaic of forest patches at different successional stages (Chambers *et al.* 2013). Because of their greater frequency, relatively small-sized patches dominate the landscape.

Tree damage and mortality occur when wind and rain loads exceed the mechanical stability of trees, leading to snapping and uprooting (Ribeiro *et al.* 2016; Peterson *et al.* 2019). In the Amazon, winds, and rain interact with different forest types that may harbor more than 280 tree species in a single hectare (de-Oliveira *et al.* 1999). In these heterogeneous forests, storm mortality can be controlled by biotic and abiotic factors (e.g., within species and across topography), with severely damaged areas experiencing up to 90% tree mortality (Magnabosco Marra *et al.* 2014; Rifai *et al.* 2016) (Figure 5.6B). The forest can lose its typical closed-canopy structure and accumulate large amounts of wood debris on the forest floor (Figure 5.6C). This gradient of gap sizes and resource/niche availability has relevant consequences for regional patterns of forest dynamics, biodiversity, and biogeochemical cycles.

Tree mortality can be selective and depends on species traits and individual characteristics (Ribeiro *et al.* 2016; Magnabosco *et al.* 2014; Rifai *et al.* 2016). Snapping and uprooting of large individual trees can topple neighbors, altering the number and size distribution of trees and reducing stand biomass. Mortality rates among surviving trees are higher in the first years following the event, slowing biomass recovery. Resprouting and growth of survivor trees contribute little to biomass recovery, which can take decades (Magnabosco Marra *et al.* 2018). Recovery trajectories differ with the severity of mortality. However, even low severities trigger secondary succession, with substantial species turnover and dynamics distinct from those observed in small treefall gaps and human forest clearing (Chambers *et al.* 2009b; Magnabosco Marra *et al.* 2014, 2018). Soil organic carbon can also increase as a function of blowdown severity due to the decomposing organic matter available from wood debris (dos-Santos *et al.* 2016).

Blowdowns can also promote tree diversity by providing niches to a diverse cohort of species that differ widely in their requirements and recruitment strategies (Magnabosco *et al.* 2014; Chambers *et al.* 2009). Nonetheless, altered functional composition indicates that blowdowns may affect the resilience of biomass stocks by favoring soft-wooded species with shorter life spans, which are also more vulnerable to future disturbances (Magnabosco Marra *et al.* 2018; Trumbore *et al.* 2015). The impacts of blowdowns can be more pronounced in secondary and fragmented forests with altered composition and structure, and a relatively higher proportion of exposed edges (Silvério *et al.* 2019; Schwartz *et al.* 2017). That aspect is critical since these account for large areas of the remnant forests in highly deforested regions of the Amazon (Brando *et al.* 2014; Hansen *et al.* 2013).

Research has focused on detecting blowdowns and quantifying their local to regional impacts on species composition, and forest structure and dynamics. However, the effects of blowdowns on forest functioning at the landscape scale are still poorly understood. Assessing the return frequency of disturbances and the recovery rates of biomass and functional composition in different regions is critical to understanding variations in carbon balance at broader spatial scales. Climate change projections indicate that the frequency and intensity of convective storms could increase in the Amazon (Negrón-Juárez *et al.* 2017; McDowell *et al.* 2018; IPCC Climate Change 2014). Determining the possible thresholds of disturbance severity under these shifting disturbance regimes is thus critical, since it will affect the future vulnerability and resilience of the Amazon forest (Trumbore *et al.* 2015; Turner *et al.* 2010). The effects of forest blowdowns on other taxa remain unassessed in the Amazon.

5.3.6.2 Lightning, natural fires, and impacts on vegetation structure and biome distribution Lightning is an impressive and common phenomenon in the Amazon due to the meteorological systems that occur there, such as the squall lines and the SACZ. Natural fires can happen when electrical storms develop in conditions where vegetation is dry, especially when cloud-to-ground lightning is accompanied by little precipitation (conventionally ≤2.5 mm) (Viegas 2012; Nauslar *et al.* 2013). This phenomenon, known as “dry lightning” or “dry thunderstorm”, also happens when the rain evaporates before reaching the ground, if a storm moves quickly, or if cloud-to-ground lightning occurs outside the region where precipitation occurs (Dowdy and Mills 2012).

Natural causes have been reported as important for ignition in the Cerrado, mainly due to cloud-to-ground lightning during the transition between dry and rainy seasons (Ramos-Neto and Pivello 2000). There is still no conclusive information on the proportion of human versus natural causes, but natural fires are believed to be around 1-2% of total fires (Alvarado *et al.* 2018).

The transition between the Amazon and Cerrado in Brazil has the largest area of contact between forest and savanna in the tropics, and these biomes differ fundamentally in their structural characteristics and species composition (Torello-Raventos *et al.* 2013). In this transition, rainfall seasonality and fire disturbances have an important ecological effect on the vegetation structure and composition due to influences on the ecological and biogeochemical processes of vegetation directly affecting the Net Primary Production and respiration that, over time, lead to changes in composition and structure of vegetation (Alves *et al.* 1997). Fires change plants' phenology and physiology, modify competition among trees, and lower canopy plants such as grasses, shrubs, and lianas. Depending on its frequency and intensity, fire may increase trees' mortality and transform an undisturbed forest into a disturbed and flammable one (House *et al.* 2003; Hirota *et al.* 2010; Hoffmann *et al.* 2012). Tree species associated with forest or savanna vegetation differ in numerous physiological characteristics, such as fire survivorship (Hoffmann *et al.* 2009; Ratnam *et al.* 2011) and their wood and foliar characteristics (Gotsch *et al.* 2010).

Couto-Santos *et al.* (2014) demonstrated the effects of climate variability and fire occurrence on forest-savanna boundaries in Roraima, in the northern part of the Brazilian Amazon. In wet years, the forest advanced over the savannas, while in years with lower rainfall, the forest receded, and the savanna expanded due to the increased frequency of drought and fire.

5.4 Evapotranspiration

When rainwater reaches the rainforest's land surface, most of it infiltrates into the soil, increasing soil moisture. About 50% of the rainfall returns to the atmosphere as evapotranspiration (ET: plant transpiration plus water evaporation from free water surfaces and bare soil; see Table 1). The remainder supplies the groundwater pool, which ultimately contributes to the formation of the Amazon Basin’s streams and rivers. This section discusses the seasonal patterns of ET and their controlling mechanisms. The role of ET as a source of water to the atmosphere, and consequently for the processes of rain formation, is discussed in Chapter 7.

An early attempt to characterize Amazonian ET was made during the Amazon Region Micrometeorological Experiment (ARME), a British-Brazilian experiment. Starting in 1983, this campaign made several micrometeorological measurements at the Ducke Reserve, about 30 km northeast of Manaus. Using ARME´s data and the Penman-Monteith equation, Shuttleworth (1988) showed a small seasonality in ET, with peaks in March and September that coincided with net radiation (Rn) extremes. The study also found that actual ET rates were nearly equal to potential ET rates throughout the year, suggesting plenty of water availability even during dry periods.

Starting in the late 1990s, during the Large-Scale Biosphere-Atmosphere project (LBA), a network of intensive eddy-covariance (EC) measurements was set up throughout the lowland Amazon to quantify surface energy, water, and carbon fluxes under different land covers (Keller *et al.* 2004). Data analysis from the EC flux towers revealed different ET seasonality depending on the study site. Most of the sites showed a seasonal pattern similar to that observed at Manaus during ARME – i.e., ET in phase with Rn, maintaining either a constant flux or showing a slight increase during the dry period compared with the rainy season (Costa *et al.*, 2004; Hutyra *et al.* 2005; Juárez *et al.* 2007; da Rocha *et al.* 2004; Sommer *et al.* 2003; Souza-Filho *et al.* 2005; Vourlitis *et al.* 2002). A few studies, mostly located in the Southwestern Amazon (Aguiar *et al.* 2006) or at the transition between Amazon forests and cerrado savannas (Borma *et al.* 2009), observed higher ET in the rainy season compared with the dry season.

Syntheses of flux tower observations across the Amazon (Costa *et al.* 2010; Hasler and Avissar 2007; Juárez *et al.* 2007), comparisons of the Amazon with other biomes (da Rocha *et al.* 2009), and a pantropical analysis (Fisher *et al.* 2009) helped elucidate the seasonal and spatial variability of Amazonian ET. Hasler and Avissar (2007) found strong seasonality in ET for the stations near the equator (2°S-3°S), with ET increasing during dry periods (June-September) and decreasing during wet periods (December-March), both correlated and in phase with Rn. In stations located further south

(9°S-11°S), ET and Rn did not present clear seasonality. These studies found the best correlations between ET and Rn at these sites during wet periods, but no correlation during dry periods. The authors attributed this response to water stress during dry periods, especially at the drier southern sites.

Negron-Juarez *et al.* (2007) analyzed ten LBA sites and concluded that all of them had higher ET during the dry period than during the rainy period. Fisher *et al.* (2009) analyzed 21 pan-tropical sites and observed an increase in ET in the dry period compared to the rainy period, with Rn explaining 87% of monthly ET variance. Da Rocha *et al.* (2009) analyzed ET data from EC flux towers at seven sites, four of them located in the northern Amazon Basin and three in the Cerrado (semideciduous forest, transitional forest floodplain, and cerrado). They observed that the seven sites analyzed could be divided into two functional groups in terms of ET seasonality. The southernmost sites, generally drier and with a longer dry season, showed decreased ET in the dry period compared to the rainy period. Minimum ET values of 2.5 mm/day were observed in transitional forests, and a minimum of 1 mm/day was observed in the cerrado sites. The northern and more humid sites, with dry season length under four months, showed the opposite pattern, with increased ET in the dry season and maximum values of around 4 mm/day. ET, Rn, and vapor pressure deficit (VPD) were positively correlated at these sites, suggesting that atmospheric conditions exert control over ET. However, it is important to consider that the most seasonal sites studied by da Rocha *et al.* (2009) had a predominance of deciduous and semi-deciduous vegetation. In these sites, the falling leaves in the dry period may have exercised important controls over ET, together with climatic conditions.

Costa *et al.* (2010) analyzed three evergreen rainforest wet equatorial sites (2°S-3°S) and two seasonally dry rainforest sites (at about 11°S). They observed that, in general, dry season ET is greater than rainy season ET. Following previous studies, they found that Rn was the main controlling factor of ET in wetter sites, followed by VPD and aerodynamic resistance. They identified different controlling factors of ET in wet and seasonally dry sites. While ET seasonality in humid equatorial forests was controlled only by environmental factors (i.e., abiotic controls), in seasonally dry forests ET was controlled by biotic parameters (e.g. stomatal conductance, gs), with surface conductance varying by a factor of two between seasons.

Observational studies generally agree on the seasonal pattern of ET in the Amazon rainforest, where ET is strongly dependent on net radiation (Rn) for seasonally humid forests. In the early 2000s, however, most models still simulated ET as being in phase with precipitation (Bonan 1998; Werth and Avissar 2004; Dickinson *et al.* 2006), suggesting that water availability limits ET. Around 2010, the LBA Data-Model Intercomparison Project (LBA-DMIP) compared the results of 21 land surface and terrestrial ecosystem models to the comprehensive observational dataset from the LBA network of flux towers to evaluate how well the new generation of models could reproduce the Amazon rainforest and Cerrado functions (de Gonçalves *et al.* 2013). As part of this project, Christoffersen *et al.* (2014) concluded that models have improved in their capacity to simulate the magnitude and seasonality of ET in equatorial tropical forests, having eliminated most dry-season water limitation. Their performance diverges in transitional forests, where seasonal water deficits are greater, but mostly capture the observed seasonal depressions in ET seen in the Cerrado. Many models depended only on deep roots or groundwater to mitigate dry season water deficits. Some models were able to match the observed ET seasonality, although they simulated no seasonality in stomatal conductance (gs). Some of these deficiencies can be improved by parameter tuning, but in most models these findings highlight the need for continuous process development (Christoffersen *et al.* 2014).

In summary, ET is controlled by the balance between water demand imposed by the atmosphere (aboveground conditions) and the water supply in the soil (belowground conditions). Both are considered abiotic controls (Costa *et al.*, 2010) or ecohydrological mechanisms (Christoffersen *et al.* 2014). By opening and closing stomata, plants may exercise important additional controls over evapotranspiration fluxes through stomatal canopy conductance (Costa *et al.* 2010; Christoffersen *et al.* 2014), resulting in a balance between photosynthesis and transpiration (Beer *et al.* 2009; Lloyd *et al.* 2009). These biotic (Costa *et al.*, 2010) or ecophysiological (Christoffersen *et al.* 2014) control mechanisms over ET and their importance in the context of regional climate will be discussed in detail in Chapter 7 (Section 7.2.2).

5.5 Main characteristics of the surface hydrological systems in the Amazon

The Amazon River Basin (including the Tocantins River as a tributary and other coastal basins) drains about 7.3 million km^2 and discharges about 16-22%% of all global river inputs to the oceans (Richey *et al.* 1989; see also Box 5.1). This vast hydrological system is formed by the Andes, the Guiana and Brazilian shields, and the Amazon plain (Sorribas *et al.* 2016). As a consequence of the seasonal rainfall cycle (Section 5.2.2), the main stem Amazon River and its tributaries exhibit high and low river levels a few months after the preceding wet and dry seasons.

In general, rivers in the southern Amazon Basin (e.g., Solimões, Madeira, Xingu, Tapajós, Tocantins-Araguaia) peak from April–May, whereas rivers in the northern Amazon (e.g., Japura-Caquetá, Rio Negro) peak from May–June (Espinoza *et al.* 2009a, b, Marengo and Espinoza *et al.* 2016). At annual time scales, the hydrological contribution of southern and northern rivers is roughly equivalent due to much higher total rainfall in the smaller northern basins compared to the larger southern basins.

5.5.1 Seasonality of discharge

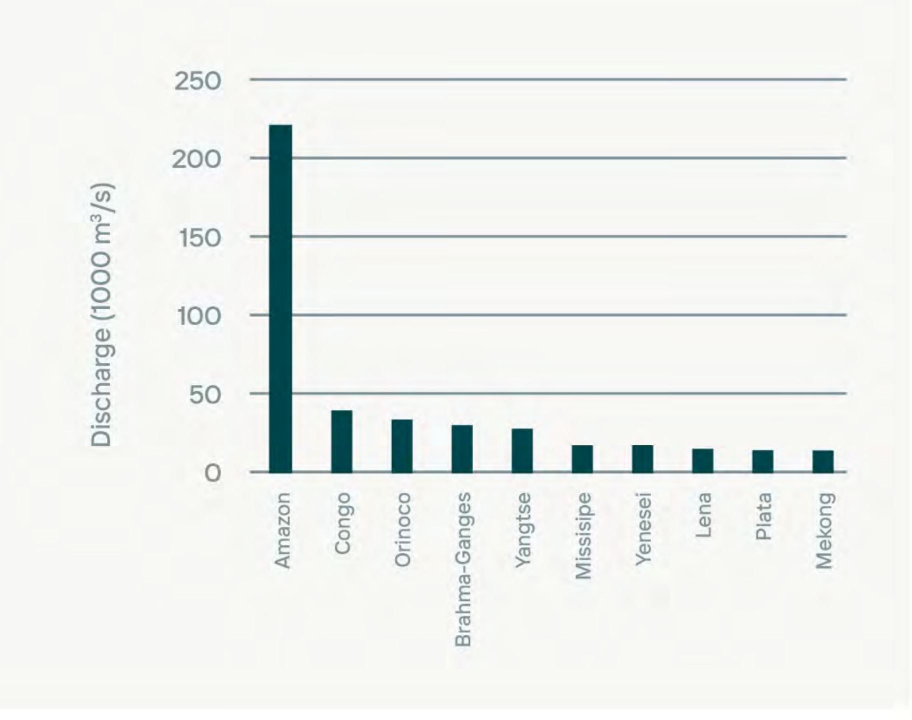
As noted above, the discharge of the mainstem Amazon River and its tributaries integrates hydrological fluctuations occurring upstream. These hydrological dynamics show a strong a few months (See Section 5.2.2), with significant variations in the timing and magnitude of discharge across the Amazon's tributary watersheds (Sorribas *et al.* 2016). The southern and western reaches of the Amazon River usually flood first, peaking between March and May. In the central Amazon, river levels are controlled by contributions from northern and southern tributaries, generally peaking in June (Figure 5.7).

Long-term discharge measurements recorded near the central Amazon city of Óbidos, for example, indicate a peak discharge approaching ~250,000 m^{3}s^{-1} during the high-water period in June, and a minimum discharge of ~100,000 m^{3}s^{-1} during the low-water period in November (Goulding *et al.* 2003).

Because the northern headwaters of the Amazon are near the equator, their water levels fall between October and February, even as the Amazon River is rising due to contributions from the large southern tributaries. Small coastal watersheds of the northern Amazon (e.g., the Araguari) are also influenced by ocean tides in their lower reaches. In contrast, most of the Amazon River's southern tributaries reach their highest levels in March or April (at points >300 km upstream from their mouths) and their lowest levels between August and October (Goulding *et al.* 2003). For example, discharge at Itaituba in the Tapajós River peaks at ~23,000 m^{3}s^{-1} in March and reaches its minimum (~5,000 m^{3}s^{-1}) in October (Figure 5.7). To its west, the Purús River at Arumã-Jusante shows even more pronounced variability, with a peak discharge of 11,000 m^{3}s^{-1} in April and a minimum discharge of ~1,000 m^{3}s^{-1} in September (Coe *et al.* 2008). The lower sections of these southern tributaries are heavily influenced by a backwater effect of the Amazon River itself, rising and falling in response to changes in the main stem (Sorribas *et al.* 2016).

BOX 5.1: How Large is the Amazon River?

"Born in the lofty, snow-clad Andes, the Amazon flows four thousand kilometers until it confronts the Atlantic at the equator. The Amazon is not only the world's longest river; it carries more water than any other river – more than ten times that of the Mississippi, for example (***Figure B.5.1.1***). One-fifth of all the water flowing off the face of the earth passes through the Amazon's mouth. Such is the force of the Amazon as it clashes with the Atlantic that it pushes a vast plume of freshwater for hundreds of kilometers into the sea. Five centuries ago a Spanish explorer traveling up the coast of Brazil noted that at a certain point the sea tasted fresh, even though his ship was out of sight of land. Pinzón dubbed that spot the sweet sea (mar dulce), which historians and geographers take to be the mouth of the river, named after women warriors in Greek mythology. The Southern Equatorial Current pushes this turbid plume, which reaches some 400 kilometers long and between 100 and 200 kilometers wide, in a northwesterly direction up the coast of Amapá and the neighboring Guianas. Because it is lighter, the freshwater overrides the salty oceans and dilutes and muddies the surface for up to one million square miles." (Quoted from Smith 2002).



Most people know that the Amazon River is the largest river of the world. What most people do not realize is just how large it really is. This figure ***Figure B.5.1.1*** compares the world's 10 largest rivers by discharge, showing the remarkable difference between the Amazon and all other rivers. The Amazon discharges about five times more water to the ocean than the world's second largest river, the Congo. The magnitude of the difference is so striking that the Amazon´s largest tributary, the Madeira – discharging about 50,000 m^3/s to the main stem – would rank second among the world's largest rivers if considered independently.

A large discharge is a direct consequence of both a large drainage area and high precipitation. The Amazon ranks first in both variables, with the largest drainage area and the highest rainfall in the world.

5.5.2 Seasonality of floodplain dynamics

Fluctuations in rainfall and river discharge drive pronounced seasonal changes in the water level of large Amazon rivers, causing them to overflow their banks into adjacent floodplains. On a local scale, flooding can also result directly from rainfall in areas with poorly drained soils or rising groundwater levels, as in the case of the Llanos de Mojos in Bolivia. The periodic rise and fall of water levels – often referred to as the seasonal flood pulse – connects rivers and their floodplains during part of the year (rivers rise between November and June, and recede between June and November), resulting in heterogeneous habitat structure, rapid recycling of nutrients and organic matter, and high rates of biological production (Junk *et al.* 2012). The Amazon River and its large tributaries are characterized by a monomodal flood pattern with an average amplitude of 10 m near Manaus, ranging from 2 to 18 m depending on the location and year (Melack and Coe 2013). The greatest annual river-level fluctuations occur in the southwestern Amazon, especially the Madeira, Purus, and Juruá Rivers, while the smallest changes happen in the east. Small (low-order) streams in the Amazon lowlands exhibit complex hydraulics, with backwater effects resulting in a less predictable polymodal hydrological regime (Piedade *et al.* 2001).

The characteristic vegetation in these flooded regions is strongly influenced by hydrological dynamics, including maximum inundation extent, flood amplitude, and the duration of the low- and high-water phases of the flood pulse. On average, the lowland rivers of the Amazon are flooded for 6-7 months out of the year, with southern tributaries flooding from January-May and northern tributaries from June to August. Conversely, the southern Amazon undergoes a pronounced dry season from August to December, which generally coincides with the low-water period. In the north, floods can last until September (Goulding *et al.* 2003). Seasonally inundated wetlands thus cover an extensive (17%) area of the lowland Amazon – estimated at 8.4×10^5 km^2 of the region <500 m above sea level (Hess *et al.* 2015). About 44% of the wetland area is located in the Madeira River and Rio Negro watersheds, the Amazon's two largest tributaries (Figure 5.2). The Marañon sub-basin has the highest proportion of total area as wetland (20%), followed by the Madeira (19%) and Içá-Putumayo (17%). The Tapajós (5%) and Xingu (8%) sub-basins have the lowest proportion of wetland (Hess *et al.* 2015).

5.6 The role of rivers in biogeochemical cycles

Rivers and related aquatic systems are key ecosystems in the Amazon region. The region's underlying geology and landscape structure determine land-water connections via hydrological flow paths that influence river flow and chemistry. In disturbed systems, hydrological dynamics are strongly influenced by the type and intensity of land use, which may alter rates of runoff, infiltration of water into soils, and water chemistry. Castello and Macedo (2015), considering river systems of different orders, stressed that soil attributes (chemical, physical, and biological) and land use are the main drivers of river biogeochemistry and metabolism. In small catchments, deforestation may increase inputs of nutrients, phosphorus, and carbon to aquatic environments, dramatically changing their natural functions. For instance, studies in small catchments identified extensive growth of an aquatic herbaceous species, leading to a high concentration of dissolved organic matter and, consequently, higher decomposition and respiration rates (Deegan *et al.* 2011).

The cascade from small to larger river systems depends on the extent of deforestation, soil type, and topography. Rivers are important providers of dissolved organic matter and nutrients to the ocean. This organic matter's chemical characteristics are key in defining its role in the coastal ocean's metabolism. The Amazon River plume has a global influence. Recent data shows that 50-76% of the dissolved organic matter carried by the Amazon to the ocean is stable (Medeiros *et al.* 2015), contributing to long-term storage of terrigenous carbon and potentially adding to the deep ocean carbon pool.

The biogeochemistry of carbon in aquatic systems involves production, transformations, and connections to terrestrial systems in environments ranging from small rivers to large river-floodplains. Small rivers, which are well connected to the surrounding watershed, are strongly influenced by riparian vegetation and biota. In the case of large rivers and their flood plains, on the other hand, the processes of carbon, nitrogen, and other nutrients are intensively modulated within the aquatic system (see also Section 6.2.2).

Changes in river flow and the frequency of floods and droughts are connected to changing climate patterns (Section 5.2), as are aquatic biogeochemical cycles. Martinelli *et al.* (2010) showed a decrease in the concentration of nitrogen species (dissolved inorganic and organic nitrogen) in aquatic systems in the Amazon with increasing river flow, but also noted the effects of changing land use and increasing population density (>10 people/km^2) in the region. One important driver of nutrient flow to aquatic systems is the soil parent material and chemistry. On weathered, heavily leached tropical soils, vegetation cover is a key component in the nitrogen and carbon cycles (Chapter 6). Nitrogen leaching to aquatic systems from “terra firme'' may vary from 3 to 6 kg N-NO_3/ha/year with stream exports of around 4 kg-N/ha/yr (Wilcke *et al.* 2013). In contrast, in flooded areas where N is exported as dissolved NO_3 and NH_4, N exports can reach up to 12 kg-N/ha/yr. Lesack and Melack (1996) analyzed the impact of deforestation on nitrogen export to the aquatic system, finding an export of 2.7 kg N-NO_3/ha/yr for upland forests along the floodplain. After partial deforestation in the same area, measurements identified a 40% increase in nitrogen export in stream water, reaching 3.6 kg N-NO_3/ha/yr (Williams and Melack 1997).

In contrast, dissolved phosphorus export is typically low. Values reviewed by Buscardo *et al.* (2016) indicate dissolved phosphorus export in streams ranging from 0.01 kg/ha/yr in a terra-firme forest (Leopoldo *et al.* 1987) to 0.006 kg P/ha/yr in an upland forest bordering a floodplain lake (Lesack and Melack 1996). Exports were an order of magnitude higher in a lower montane forest in Ecuador, reaching 0.6 kg/ha/yr (Wilcke *et al.* 2008).

5.7 Conclusions

The Amazon´s rainfall, river flow, and flood regime exhibit considerable variability at seasonal, interannual and interdecadal scales, with extreme flood and drought events becoming more common in the last two decades. Seasonal variability is mainly controlled by solar forcing. ENSO events are a major cause of interannual variation in rainfall, flow, and floodplain extent in the Amazon Basin. Central-Pacific El Niños (La Niñas) are related to rainfall deficits (excesses) over the upper part of the basin (Andean region of Colombia, Ecuador, and Peru), but these anomalies are weaker during Eastern-Pacific El Niño (La Niña) events. During Eastern-Pacific El Niño events, rainfall anomalies are stronger in the Madeira Basin. The interannual modes of variability are modulated by interdecadal modes of the nearby oceans, such as the Pacific Decadal Oscillation and the Atlantic Multidecadal Oscillation. Moreover, extreme rainfall and flooding events are not necessarily associated with ENSO events.

Interactions between large-scale atmospheric circulation and orographic induced circulations result in high spatial variability of precipitation over the Amazon-Andean region, which may reach 7,000 mm/year – the highest rainfall levels seen anywhere in the Amazon Basin. As a result of these interactions, the Andean Basins also show the largest runoff per unit area, and Andean rivers deliver sediments, pollutants, and nutrients downstream to the Amazon lowlands.

5.8 Recommendations

- The main processes of the Amazon hydroclimate system (convection, mesoscale circulations, land surface processes) are associated with the rainforest's presence. Preserving and restoring the Amazon forest is essential to maintain these processes, which are important locally, to the Andes, to South America, and globally.

- It is still unknown which factors drive recent accelerations in interannual climate variability, particularly given the interactions among deforestation, changes in atmospheric greenhouse gas concentrations, and natural modes of climate variability. Further research is needed to attribute the causes of this acceleration and to reduce uncertainties, helping to predict impacts and define conservation strategies.

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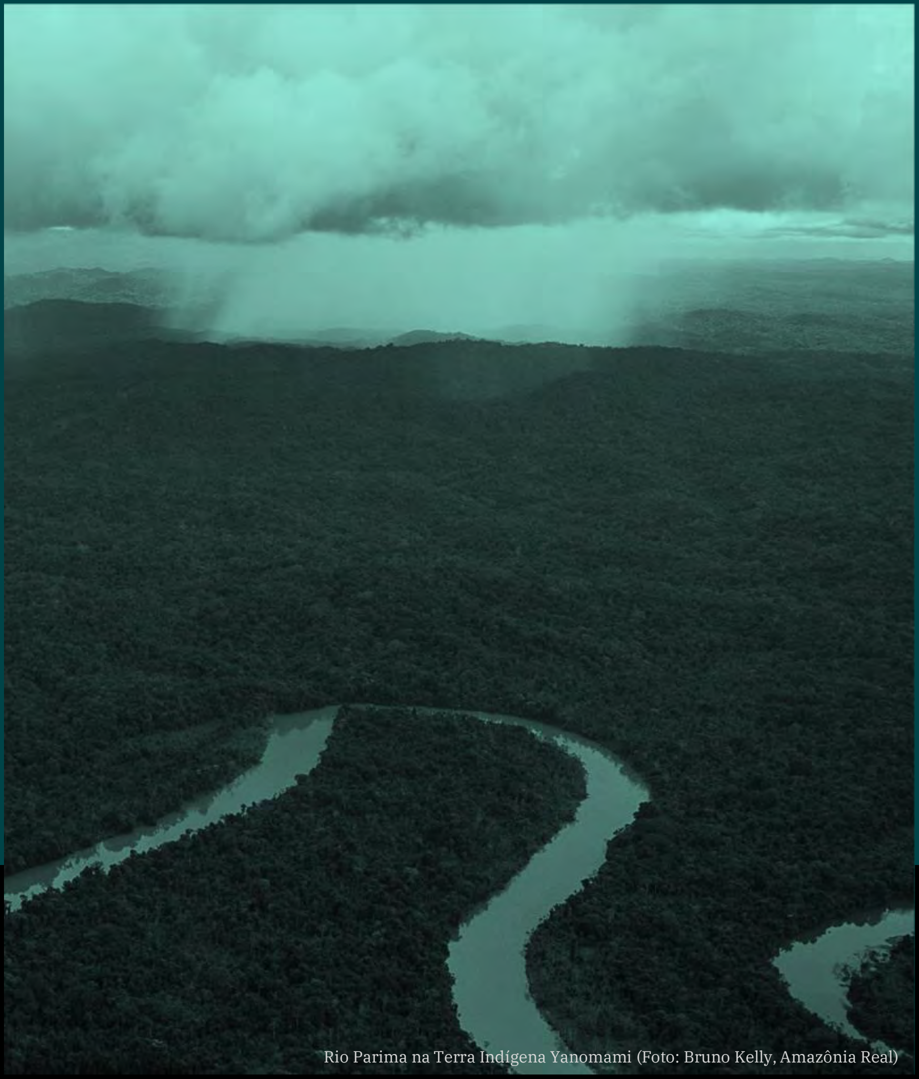
Amazon Assessment Report 2021

Chapter 6

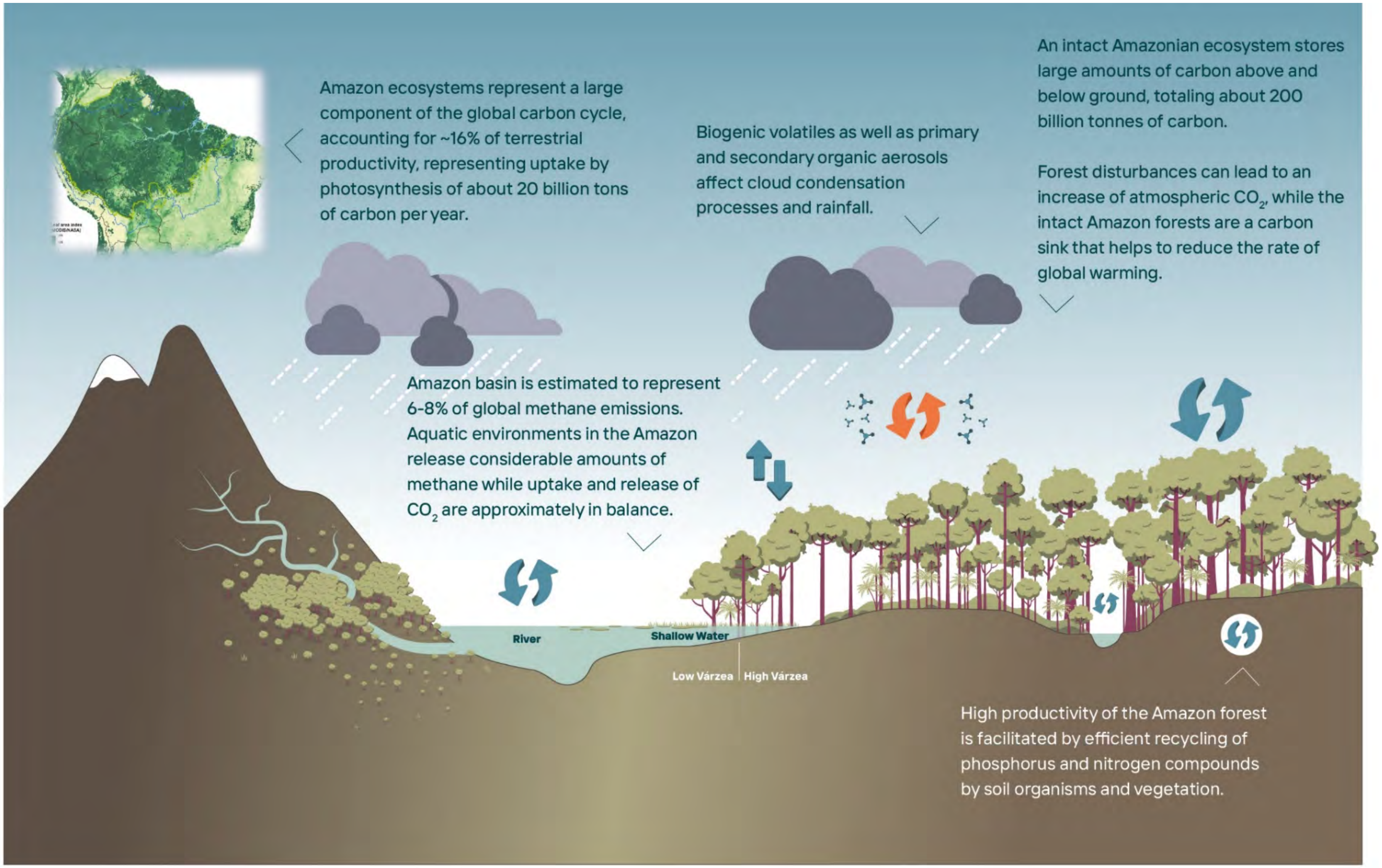
Biogeochemical cycles in the Amazon



Rio Parima na Terra Indígena Yanomami (Foto: Bruno Kelly, Amazônia Real)

INDEX

Graphical Abstract



Amazon ecosystems represent a large component of the global carbon cycle, accounting for ~16% of terrestrial productivity, representing uptake by photosynthesis of about 20 billion tons of carbon per year.

Biogenic volatiles as well as primary and secondary organic aerosols affect cloud condensation processes and rainfall.

An intact Amazonian ecosystem stores large amounts of carbon above and below ground, totaling about 200 billion tonnes of carbon.

Forest disturbances can lead to an increase of atmospheric CO_2, while the intact Amazon forests are a carbon sink that helps to reduce the rate of global warming.

Amazon basin is estimated to represent 6-8% of global methane emissions. Aquatic environments in the Amazon release considerable amounts of methane while uptake and release of CO_2 are approximately in balance.

High productivity of the Amazon forest is facilitated by efficient recycling of phosphorus and nitrogen compounds by soil organisms and vegetation.

Figure 6.A Graphical Abstract.

Biogeochemical Cycles of the Amazon

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Key Messages

- The Amazon forest is a major store and ongoing sink of carbon that makes a modest contribution to reducing carbon dioxide levels in the atmosphere. This carbon sink has been weakening over recent decades.
- Available estimates of carbon inputs from plants growing in seasonally inundated habitats are of similar order to estimates of CO_2 degassed from these habitats. Hence, aquatic environments would seem to be approximately in balance, though inputs from uplands do add some inorganic and organic carbon.
- Methane emissions from the Amazon Basin are estimated to represent 6-8% of global methane emissions, though large uncertainties in both sources and sinks remain.
- The Amazon region contributes a large fraction of global N_2O emissions from natural ecosystems; biological N fixation is a major source of available nitrogen for the regional biosphere.
- The release of biogenic volatiles from the forest plays an important role in cloud condensation, affecting rainfall.

Abstract

The Amazon basin hosts the Earth's largest extent of tropical forest and the world's largest river system. These two features make it a major contributor to regional and global biogeochemical cycles, such as the carbon cycle and major nutrient cycles. This chapter summarizes our understanding of the cycles of three key biogeochemical elements in the Amazon (carbon, nitrogen, and phosphorus), spanning both terrestrial and aquatic ecosystems. Historically, the intact Amazon biome has been a major carbon sink, though this sink appears to be weakening over time. The chapter also examines the net emissions of two other key trace gases with substantial contributions to radiative warming (methane and dinitrogen oxide), and trace gas and aerosol emissions and their impact on atmospheric pollution, cloud properties, and water cycling.

Keywords: carbon, carbon dioxide, methane, nitrogen, phosphorus, aerosols, clouds, aquatic, terrestrial

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6.1 Introduction

The Amazon basin accounts for around 16% of the entire metabolism of the terrestrial biosphere and is the largest drainage basin in the world, contributing around one-fifth of global freshwater discharge. These features make it a major contributor to regional and global biogeochemical cycles, including the cycles of carbon, nitrogen, phosphorus, and other nutrients. This chapter highlights and summarizes some of the main aspects of the biogeochemistry of the Amazon region. The focus is to understand baseline or natural biogeochemical processes in relatively intact regions of the Amazon. Deforested and other human-modified landscapes are discussed in Part II of this report. However, where we draw up budgets for the whole region (of carbon or methane), we include anthropogenic emissions in order to have a complete picture. This chapter starts with first considering the carbon cycle of Amazon, its seasonal variability, and the role of the intact Amazon forest as a carbon sink. Subsequent sections describe the cycling of key nutrients in the Amazon (nitrogen and phosphorus). Then we consider the region's contribution to global budgets of other major greenhouse gases, methane and N_2O. Finally, we turn to emissions of other biogenic trace gases and aerosols, and their role in affecting cloud physics and dynamics and ozone chemistry.

When considering the literature on the biogeochemical cycles of the Amazon region as a whole, it is important to define what is meant by the Amazon. Different studies use different definitions. For example, forest carbon cycle studies tend to focus on the whole lowland forest biome, including areas outside of the Amazon watershed (e.g., the Guyanas) but exclude non-lowland forest biomes such as the planalto and the Andean montane regions. In contrast, hydrological studies tend to focus on the entire watershed. Here, we adopt the definitions of Eva *et al.* (2005). The five regions of Amazon *sensu lato* (the whole Amazon-Tocantins watershed plus adjoining lowland forest regions) are the Amazon Basin lowland forests (5,569,174 km^2), Guyana lowland forests (970,161 km^2), Gurupi lowland forests (161,463 km^2), the non-forest biome Amazon watershed in the planalto (864,951 km^2) and the montane Andes in the Amazon watershed (555,564 km^2). The narrowest definition (lowland forest biome within the Amazon Basin) is also referred to as the Amazon *sensu stricto*. Please refer to the Annex on geographic limits and meanings for further exploration of this issue.

We first focus on forest biomass carbon dynamics; the Amazon holds a great deal of carbon in aboveground biomass; therefore, the forest and its fate are linked to the global carbon cycle. However, water availability and nutrients can limit productivity and affect carbon cycling; we discuss the water, nitrogen, and phosphorus cycles. We then focus attention on two other important greenhouse gases with significant sources in the Amazon: methane and nitrous oxide. Finally, forests are linked to climate not only through their ability to evaporate water, but through the production of gases and aerosols that in turn influence radiation, cloud properties, and precipitation. Our focus throughout is on largely intact ecosystems in Amazon, mainly forests and freshwaters, but under recent and current climate and atmospheric conditions. Hence, these intact ecosystems are not equivalent to preindustrial Amazonian ecosystems. Degraded and extensively modified Amazonian ecosystems are discussed in Part II of this report.

6.2 Carbon Cycle in the Amazon

6.2.1 The Amazon carbon cycle throughout the Cenozoic and Pleistocene

The South American broadleaf tropical forest biome probably began to take its modern, closed-canopy, angiosperm-dominated structure in the wake of the Chicxulub asteroid impact 66 million years ago, and the associated extinction of megafaunal dinosaurs (Carvalho *et al.* 2021) (see Chapter 1). In the warm, humid climates of the Paleogene (66-23 Ma), "tropical" (or megathermal, i.e. not affected by frost) forests covered much of South

America, connecting the proto-Amazon and Atlantic Forest biomes and extending much further south to Patagonia (Maslin *et al.* 2005). The suitable climate and high atmospheric CO_2 concentrations of this early "mega-Amazon" could have resulted in substantially higher productivity and overall biomass than the modern Neotropical biome. Over the last 50 million years, CO_2 concentrations have broadly declined, and there has been an associated cooling and drying of the global and regional climate. Tropical forests have retreated, the Atlantic Forest separated from the Amazonian biome (Maslin *et al.* 2005), and grasses spread from Africa in the Late Miocene (~10 Ma), resulting in the creation of new, fire-dominated savanna biomes such as the cerrado, and the further retreat of the forest (Osborne *et al.* 2007). Carbon stocks and ecosystem productivity are likely to have declined along with these atmospheric changes.

Over the Pleistocene (2.6 Ma - 11.7 Ka), the establishment of large, northern ice caps greatly amplified climate instability. These ice caps enabled ice-albedo feedbacks. Slight cooling (warming) led to further expansion (retreat) of ice sheets, leading to increased (decreased) reflection of solar radiation, and by extension amplification of small changes in Earth's rotation and orbit into dramatic changes in climate. The last 1 million years have been dominated by a roughly 100,000-year cycle, 90% of which is largely a cool climate with low atmospheric CO_2 (~180 ppm) and high climate variability, broken by short (~10,000-year periods) of warmer and wetter conditions, higher CO_2 (~280 pm), and less climate variability (the Holocene being a prime example). Low CO_2 concentrations of glacial periods (180 ppm) may be close to the threshold of viability of photosynthesis and would have reduced ecosystem productivity.

There has been much speculation as to how Amazonian forests varied during these glacial-interglacial cycles. Haffer (1969) famously suggested that during glacial maxima the forest biome retreated into refugia separated by cerrado, and this process was a driver of Amazonian speciation. This scenario has not stood the test of time; the broad consensus seems to be that during glacial periods there was only modest retreat in forest extent at the boundaries. Paleoecological and speleotherm data suggest that the climate was undoubtedly drier, but the lower temperatures reduced evapotranspiration rates and enabled forest to persist (Mayle *et al.* 2004, Bush *et al.* 2017, Wang *et al.* 2017). However, substantial areas of forest may have been dry forests interweaved between moist rainforests. The variability of the climate may have enabled an occasional corridor of savanna to open in the eastern Amazon. Overall, Amazonian carbon stocks are likely to have been only slightly reduced from present-day values, but productivity would have been substantially reduced and the rate of carbon cycling slower (Mayle *et al.* 2004).

In the latest interglacial period, the Holocene (11.7 Ka – present), rainforest productivity and carbon stocks initially increased with warmer, wetter, and higher CO_2 conditions. However, over the early- to mid-Holocene (ca. 8,500–3,600 yr BP), reduced precipitation and increased fire frequency affected much of the south of the region, resulting in forest retreat and expansion of savanna and dry forest (Mayle *et al.* 2004). In the Late Holocene, the rain belt expanded further south, and the forest gradually expanded southwards, resulting in an overall increase in the Amazon's forest biomass to peak values in the last thousand years (Mayle *et al.* 2004).

6.2.2 Carbon cycle processes in terrestrial Amazonian forests

6.2.2.1 Amazon Forest Carbon Cycle

The Amazon forest biome stores around 90 Pg C in above- and below-ground vegetation biomass (Saatchi *et al.* 2007). Soil carbon stocks are of similar magnitude to vegetation biomass carbon (Malhi *et al.* 2009, de Oliveira Marques *et al.* 2017), and hence total carbon stocks of the Amazon forest biome are ~150-200 Pg C. Some of the soil carbon is in non-labile fractions relatively resistant to forest cover loss, but a large part is in labile forms near

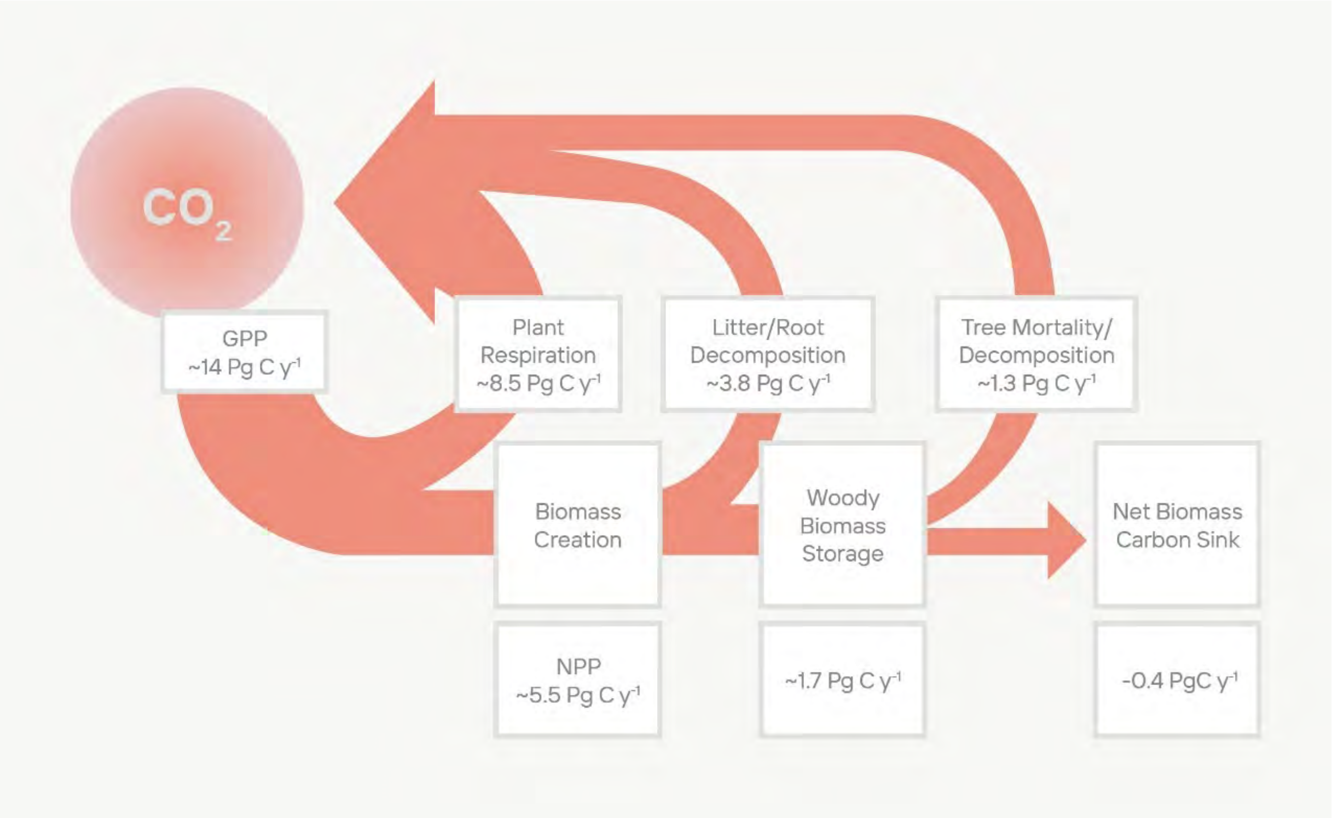

Figure 6.1 Some of the key concepts in the terrestrial carbon cycle (the numbers indicated are for the entire Amazon forest biome). Plants take up carbon dioxide through photosynthesis: this is the Gross Primary Productivity (GPP). Much of the carbon is used for plant metabolism and respiration, with the remainder being used to produce biomass including wood, leaves and fine roots. The short-lived tissue is rapidly shed and decomposed, releasing carbon dioxide back to the atmosphere as heterotrophic respiration. Carbon in woody tissue and soils tends to accumulate over time through ecological succession but is mostly released back to the atmosphere through tree mortality and decomposition. Overall, the processes of woody biomass creation and tree mortality have not been in balance in recent decades, leading to a net biomass carbon sink, equivalent to positive Net Biome Productivity (NBP). Data are extrapolated to the area of the Amazon forest biome using values provided in Malhi *et al.* (2016) and Brienen *et al.* (2015).

the surface that are vulnerable to loss (de Oliveira Marques *et al.* 2017).

The net carbon balance of terrestrial Amazonian systems is the resultant of large fluxes of uptake and release. With their year-long growing season, tropical forests such as those in the Amazon are amongst the most productive natural ecosystems on Earth. A range of studies across the basin describe the carbon cycle processes of Amazonian forests. Figure 6.2 illustrates the carbon cycle of a typical central Amazonian forest near Manaus, Brazil, derived from (Malhi *et al.* 2009).

Input of carbon to the forest through photosynthesis is termed gross primary productivity (GPP); typically, about one-third of GPP is used for biomass production of wood, fine roots, leaves, and reproductive tissues (net primary productivity or fine root tissues are short-lived and make up a small proportion of total biomass stocks. All biomass ends up as dead material, either through litterfall, herbivory, or mortality. This material is broken down and metabolized, primarily by fungi but also by bacteria and soil macrofauna such as termites, releasing carbon dioxide to the atmosphere as heterotrophic respiration. There are additional, sma-

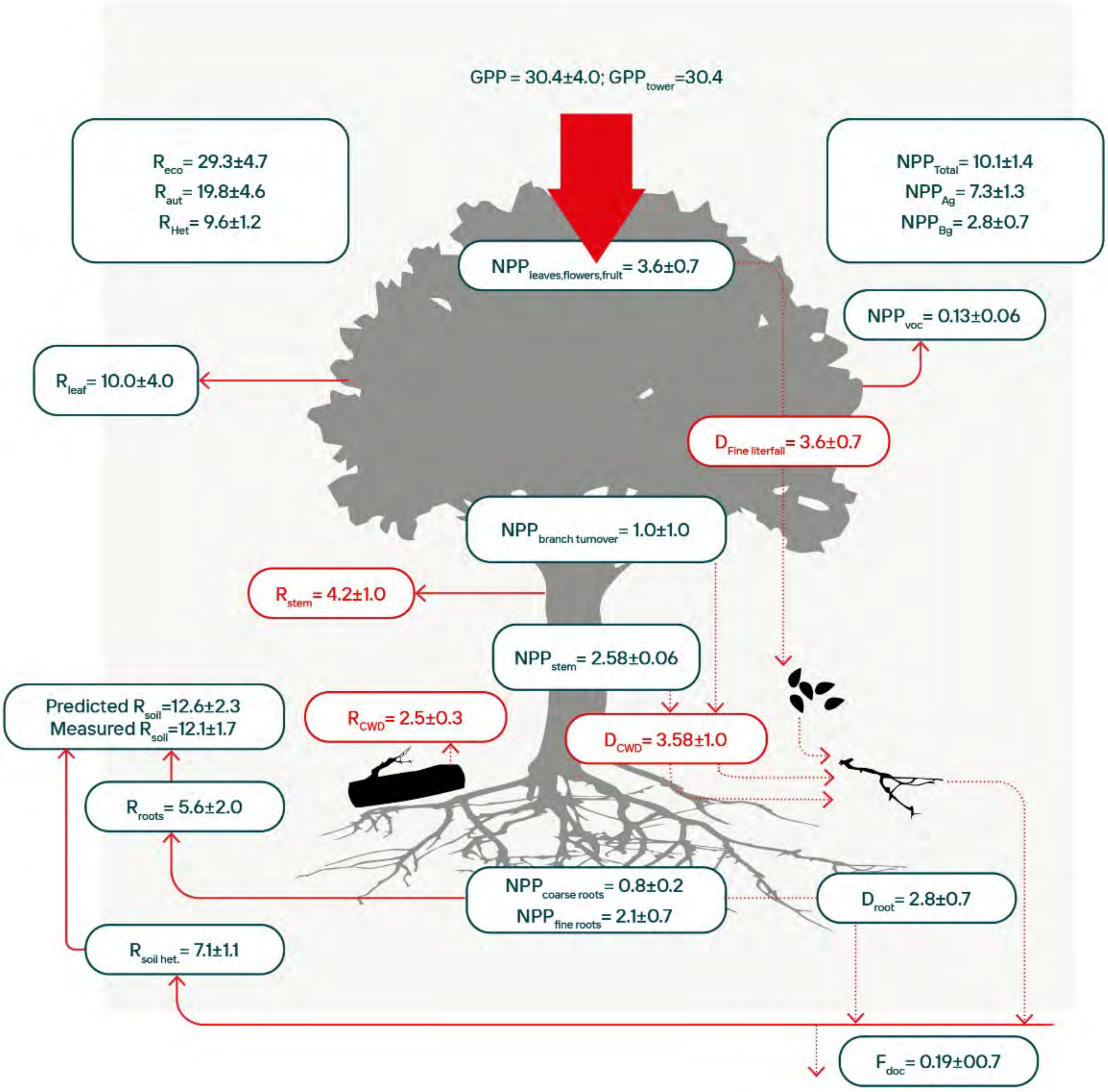

Figure 6.2. The carbon cycle of a typical Amazonian forest (near Manaus, central Amazon). Adapted from data in Malhi et al. (2009a). GPP = Gross Primary Productivity (predicted as sum of NPP and autotrophic respiration, and directly estimated from flux tower measurements (NEE + Reco); NEE - net carbon flux or net ecosystem exchange, Reco - combination of autotrophic and heterotrophic respiration, NPP - Net Primary Productivity, in total, and above ground (AG) and belowground (BG) components, and its components as (i) canopy production (leaves, flower, fruit, twigs); (ii) branch turnover; (iii) volatile organic carbon emissions (VOC); (iv) above-ground woody tissue production (stem); (v) coarse root production; (vi) fine root production; R - Respiration, in total and autotrophic (aut) and heterotrophic (het) components, and its components as (vii) leaf respiration; (viii) wood tissue respiration; (ix) root respiration; (x) soil heterotrophic respiration; (xi) total soil respiration, either directly measured or predicted as sum of inputs assuming no net change in soil carbon stocks; D - detritus fluxes, as (xii) fine litterfall; (xiii) coarse woody debris production; (xiv) root detritus production; (xv) Fdoc - carbon export in the form of dissolved organic carbon. Units are Mg C ha^{-1} y^{1}.

ller fluxes to and from the ecosystem; volatile organic compounds, such as isoprenoids (isoprene, monoterpenes, sequiterpenes), and methane account for more than 0.5% of GPP (Kesselmeier *et al.* 2002), and outflow of dissolved organic carbon in stream water is less than 1% of GPP, though this fraction will vary by soil and vegetation and is not well sampled. The net carbon balance of a mature *terra firme* Amazonian forest could be expected to be zero from ecological first principles, as the uptake of carbon through photosynthesis is compensated by releases of carbon through heterotrophic and autotrophic respiration. However, long term inventories suggest a net rate of increase of vegetation biomass of 0.6 Mg C ha^{-1} y^{-1} (where Mg is 10^6 grams) (see below), equivalent to about 2% of photosynthesis (Brienen *et al.* 2015).

6.2.2.2 Variation of GPP and NPP Across the Amazon and Their Relation to Climate, Geology, and Hydrology

The total GPP of the Amazon is around 20 Pg C y^{-1}, accounting for around 16% of global terrestrial GPP (Beer *et al*. 2010). There are relatively few direct measurements of NPP and GPP across the Amazon. Broadly, the magnitude of GPP is determined more by seasonality in rainfall rather than soil nutrient status, with the highest values found in the wet forests of the northwestern Amazon, and lower values in regions with a long dry season, where photosynthesis rates in the dry season are reduced by either stomatal closure or by increasing deciduousness (Malhi *et al*. 2015). The highest productivities reported for the Amazon are in the aseasonal and relatively fertile forests near Iquitos in Peru (Malhi *et al*. 2015). Sandy soils, such as those found in the upper Rio Negro Basin, support lower productivity. However, rates of NPP and woody biomass production do not follow the same regional pattern, and higher rates of woody growth tend to be found in the western Amazon. This may be because the soils of the western Amazon tend to have higher nutrient content (Malhi *et al*. 2004), reflecting their younger age, geological history, and soil structure (Quesada *et al*. 2012). There is a strong gradient in tree turnover across the Amazon, with trees in the western and southern Amazon tending to both grow faster and die younger, and trees in the eastern Amazon (and especially the Guyana shield) being slow-growing and long-lived (Quesada *et al*. 2012). This change in dynamics affects the patterns of biomass, with the highest biomass (and vegetative carbon stock) in Amazonian forests tending to be found in the northeastern Amazon (Johnson *et al*. 2016). Hence, in mat ure forests, rates of tree growth are negatively correlated with forest biomass, and tree mortality and turnover rates influence biomass more strongly than productivity and tree growth rates. In montane systems in the Andes, the productivity of forests declines with elevation, halving by about 3,000 m elevation (Malhi *et al*. 2018). Forest turnover rates show no trend with elevation, so forest biomass declines in proportion to declining productivity.

Both the magnitude and nature of soil carbon stocks are highly variable across the Amazon. Soil types range from highly-weathered ferralsols which dominate the eastern parts of the Basin, through to a predominance of younger soils in the western basin and lower montane slopes, occasional patches of sandy soils, and carbon-rich organic soils dominating in wetland regions, such as northern Peru, and montane cloud forests (Quesada *et al*. 2020).

6.2.2.3 Seasonal Variation of the Carbon Cycle

Plant phenology — the timing of cyclic or recurrent biological events, such as leaf, stem, or root growth; leaf senescence; or flowering — is a sensitive indicator of plant and forest function that links seasonal climate rhythms to the seasonality of carbon cycle processes (Albert *et al.* 2019, Reich *et al.* 2004, Jones *et al.* 2014, Saleska *et al.* 2003). The seasonality of GPP fluxes emerges from the phenology of leaf growth and senescence (Wu *et al.* 2016, Lopes *et al.* 2016, Wagner *et al.* 2017), while that of soil respiration is likely linked to climate seasonality and the phenology of both leaves and fine root dynamics (Keller *et al.* 2004, Raich 2017, Girardin *et al.* 2016). Seasonality of soil respiration is also buffered by deep soil CO_2 production, which lags surface soil CO_2 production due to slower drying of deep soil horizons in the dry season (Davidson *et al.* 2004). Understanding how seasonal rhythms of biology, climate, and resources interact to regulate carbon fluxes is thus a key part of understanding and predicting forest drought response, resilience, and future change.

GPP seasonality exhibits distinct patterns across the Amazon; including a notable contrast readily seen from space, ground surveys, or eddy flux towers; between dry season increases in GPP ("greening") in intact rainforest regions of the central Amazon versus seasonal declines ("browning") in converted forests, southern forests, or savanna woodlands (Figure 6.3). There is debate over these patterns and the mechanisms driving them (including whether they might be remote sensing artefacts (Huete *et al.* 2006, Morton *et al.* 2014, Saleska *et al.* 2016), and how they might be modeled (Lee *et al.* 2005, Baker *et al.* 2008, Restrepo-Coupe *et al.* 2017), but recent work combining flux data, satellites, phenocams, and leaf-level data suggests they emerge from patterns of water availability (Guan *et al.* 2015) and root distribution (Ivanov *et al.* 2012; Brum *et al.* 2019), sunlight (Restrepo-Coupe *et al.* 2013), and plant phenological strategy (Wu *et al.* 2016, Wagner *et al.* 2017).

Seasonal variation in biosphere functioning couple carbon and water exchanges with the atmosphere and contribute to global scale seasonal variations in atmospheric CO_2 and H_2O. Because leaf stomata link evapotranspiration to GPP, dry season maxima in GPP facilitate a corresponding dry season maxima in forest ET (Shuttleworth 1988, Hasler and Avissar 2007; see Chapter 7). By moistening the dry season atmospheric boundary layer, these fluxes hasten the transition to the wet season ahead of the southward migration of the intertropical convergence zone (Wright *et al.* 2017, Fu and Li 2004).

6.2.2.4 The net carbon sink in intact Amazonian forests

Old-growth forests are, in principle, in long-term equilibrium, with woody biomass growth balanced by mortality, and photosynthesis equal to the sum of autotrophic and heterotrophic respiration plus a minor amount exported to streams and rivers (Figure 6.2), with a net carbon balance of zero. In practice, an old-growth forest stand may not be carbon neutral because of (i) long term episodic disturbance and recovery; (ii) large, long-lived trees that may continue to accumulate biomass for many centuries or even millennia; (iii) secular atmospheric changes, such as rising CO_2 concentration, or changes in temperature or rainfall may lead to long-term trends in productivity and/or respiration. The RAINFOR network has monitored aboveground biomass changes in Amazon, and currently spans over 400 plots across the region. The network's observations suggest an increase in biomass in old growth forests over time, summing to 0.38 (0.28-0.49 95% C.I.) Pg C year^{-1} if extrapolated over the Amazon forest biome in the 2000s (Brienen *et al.* 2015) (Figure 6.4). This accumulation seems to stop in drought years (Phillips *et al.* 2009) and seems to be declining over time (Brienen *et al.* 2015). Increasing length of the dry season may lead to the intact forests of the Amazon becoming a carbon source in the near future (see Chapter 19). The widespread nature of the observed biomass accumulation (plus similar observations from Africa and Borneo) suggests that a global driver such as increasing atmospheric CO_2 could be responsible for this net carbon sink (Hubau *et al.* 2020, Qie *et al.* 2019). An alternative possibility is recovery from past anthropogenic disturbance (with accessible sites more likely to have been disturbed in the past), although the timescales involved (>100 years) and the observation of increasing growth rates over time argue against this possibility.

6.2.2.5 The Amazon's contribution to atmospheric oxygen

Terrestrial carbon fluxes are mirrored by oxygen fluxes; photosynthesis absorbs carbon from the atmosphere and releases an equivalent number of molecules of oxygen, and respiration releases carbon dioxide and consumes oxygen. As intact Amazonian forests are currently a net carbon sink, as described above, they must be a net oxygen source.

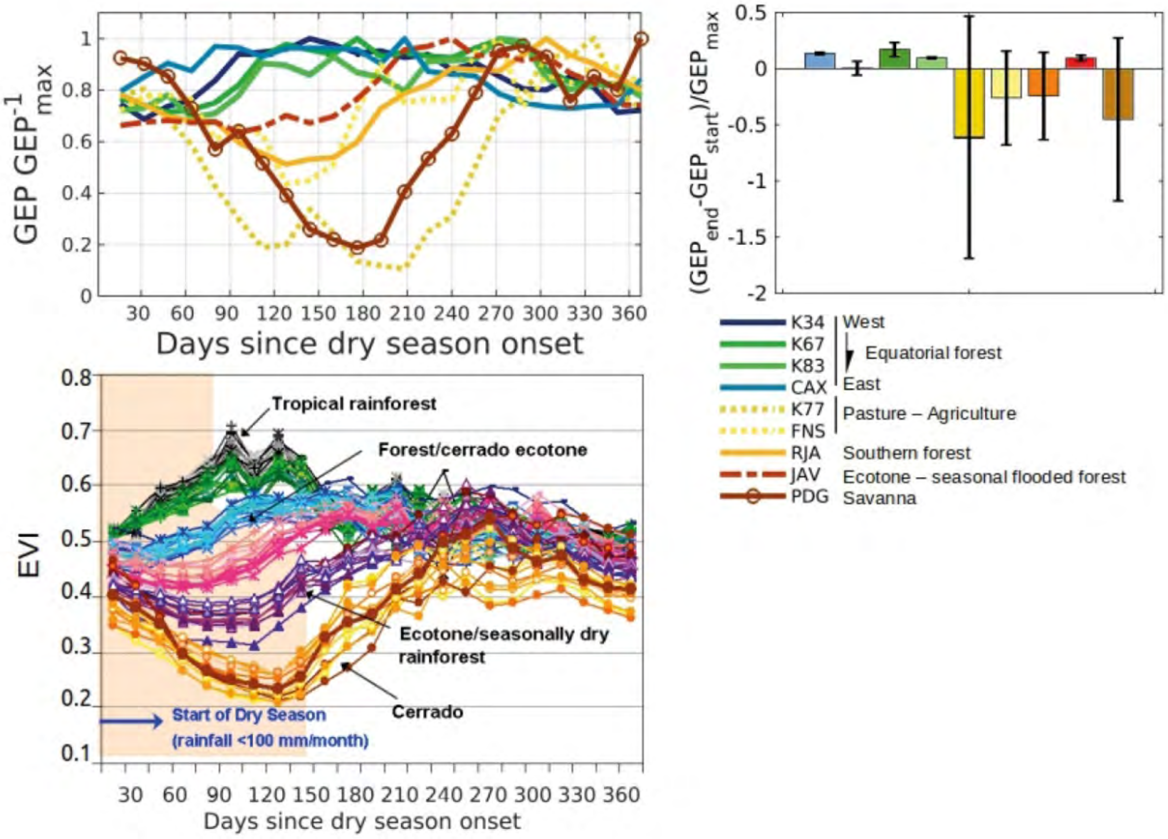

Figure 6.3 (upper left panel) Dry season gross primary productivity (GPP), photosynthetic flux, relative to maximum at each site ($GPP\ GPP_{max}^{-1}$) dynamics versus number of days since dry-season onset, across different sites in Amazon (see legend to the right, with equatorial forests in green/blue solid lines, southern forest orange line, pastures as dotted yellow lines, ecotone forest as dashed, and cerrado in solid brown). (upper right panel) GPP fractional change during the dry season, relative to its magnitude at start of the dry season (error bars indicate site-specific interannual variability) (modified from Restrepo-Coupe *et al.* (2013)). (lower panel) MODIS enhanced vegetation index (EVI) across an ecotone from Santarém forests to cerrado near Cuiabá (modified from Ratana *et al*. 2012, 2006).

This has led to the widespread perception that the Amazon is essential to the oxygen supply, and that losing the Amazon forest would lead to a significant decrease in oxygen. This perception is incorrect. The crucial difference between carbon dioxide and oxygen is that the current atmospheric stock of CO_2 is ~415 ppm, whereas the current atmospheric oxygen stock is ~21%, or 21,000 ppm. Hence a rate of increase of CO_2 of 2 ppm per decade (the approximate contribution of tropical deforestation) is significant (~0.5% per decade), but the corresponding decrease of oxygen (~0.002% per decade) is negligible. On the timescale of thousands of years the Amazon is likely in approximate net carbon and oxygen balance, with photosynthesis balanced by respiration; large stocks of atmospheric oxygen were instead built up over millions of years mainly by ocean phytoplankton. There are many reasons for concern for the Amazon, but loss of oxygen is not one of them.

6.2.3 Disturbances as Modifiers of the Amazonian Carbon Cycle

The steady state of the Amazonian carbon cycle can be disrupted abruptly, with long-lasting effects, by forest disturbances, both natural and anthropogenic. These can be associated with climate-driven intensification of seasonal cycles (Barichivich *et al.* 2018, Gouveia *et al.* 2019), which can be exacerbated by the interaction between deforesta-

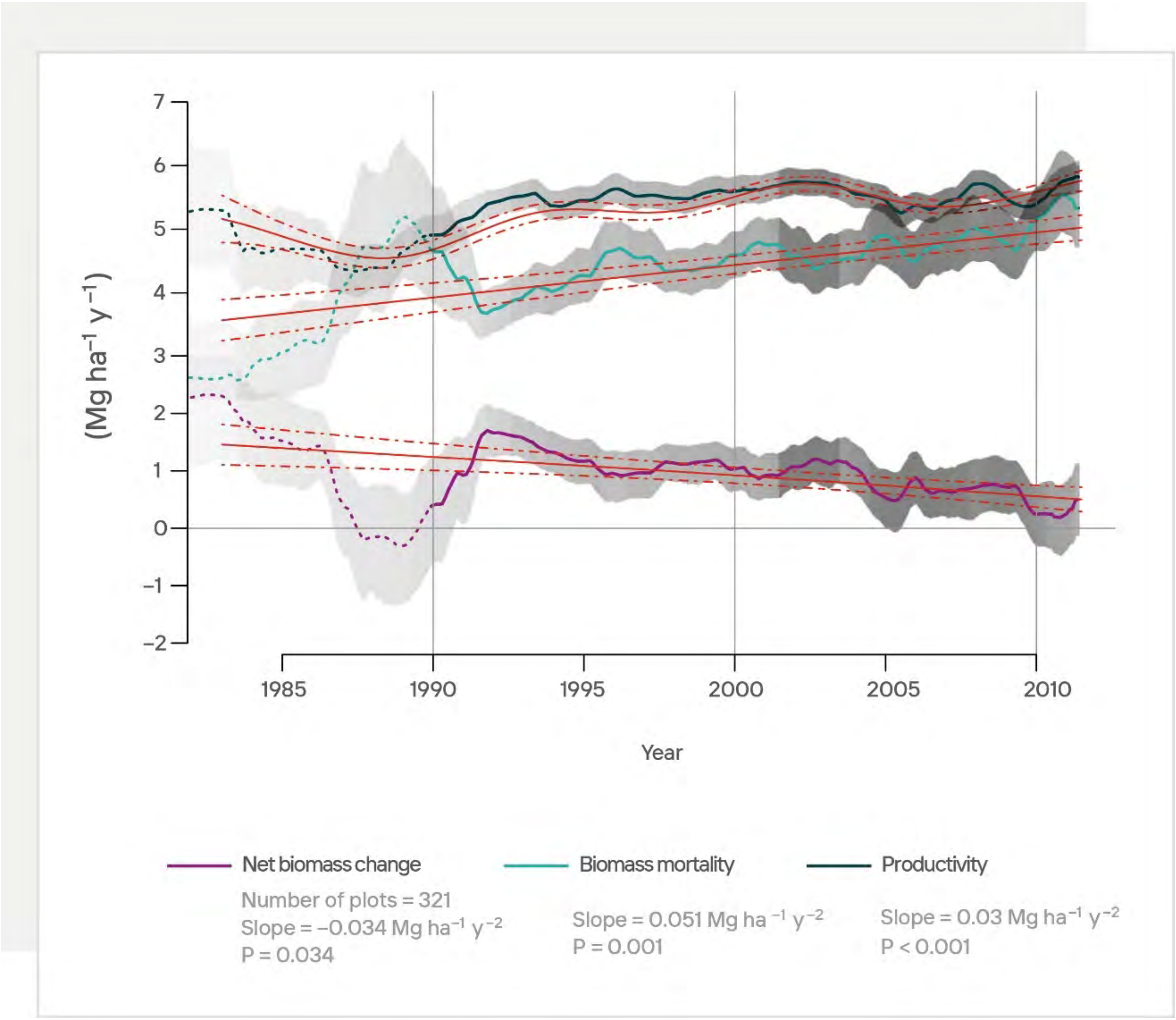

Figure 6.4. Long-term carbon dynamics of structurally intact old growth tropical forests in Amazon (adapted from Brienen *et al.* 2015) Trends in net aboveground live biomass carbon (a), carbon gains to the system from wood production (b), and carbon losses from the system from tree mortality (c), measured in 321 forest inventory plots. Black lines show the overall mean change up to 2011 for 321 plots (or 274 units) weighted by plot size, and its bootstrapped confidence interval (shaded area). The red lines indicate the best model fit for the long-term trends since 1983 using general additive mixed models (GAMM), accounting explicitly for differences in dynamics between plots (red lines denote overall mean, broken lines denote standard error of the mean).

tion and climate change (Zemp *et al.* 2017), increasing the frequency of flooding, windstorms, and droughts. On the other hand, changes in the frequency and intensity of extreme climatic events, especially droughts, can favor human-induced forest disturbances related to human-ignited fires, which can lead to forest degradation. The combination of climatic and anthropogenic processes tend to reinforce each other (Cochrane 2001; Cochrane & Laurance 2002, 2008; Alencar, Solorzano & Nepstad 2004; Aragão *et al.* 2007, 2008; Poulter *et al.* 2010, Zemp *et al.* 2017), exacerbating any single forcing impact.

6.2.3.1 Direct Climate Effect on the Carbon Cycle

Blowdowns are meteorological processes caused by downbursts associated with convective squall lines, resulting in large patches of tree mortality by uprooting or breaking tree trunks (Espirito-Santo *et al.* 2014, Araujo *et al.* 2017). These events can cause significant gross losses of carbon from aboveground live biomass, with large (≥5 ha, blowdowns only) and intermediate (0.1–5 ha, blowdowns plus other causes of death) events contributing to ~0.3% (~0.003 Pg C y^{-1}), and ~1.1% (~0.01 Pg C y^{-1}) of the loss. Most of the natural gross C loss, however, is concentrated in small (<0.1 ha) canopy disturbances accounting for ~98.6% (~1.28 Pg C y^{-1}) of total forest-dynamics related losses over the entire Amazon region (Figure 6.1; Espirito-Santo *et al*. 2014, where Pg is 10^{15} g). Despite the magnitude of impacts on C stocks, recovery of disturbed patches promotes net biomass accumulation that approximately balances observed losses. Forests disturbed by blowdowns tend, however, to be more susceptible to the effects of other forest disturbances, such as droughts and fires. The impact of droughts may be larger in these forests due to changes in plant community composition and structure, favoring early successional species with fast growth rates (Nelson *et al*. 1994), which are characterized by low wood density and susceptibility to drought (Phillips *et al*. 2009, 2010). The accumulation of dead wood from tree mortality can further destabilize the C cycle by increasing forest vulnerability to fire, if these areas are near human-ignition sources.

The frequency of interannual climate variations (e.g., recurring droughts or periods of excess wetness due to El Niño and the Southern Oscillation (ENSO) cycles, and associated occurrence of fires or blowdowns) structure Amazonian forests' functional composition and carbon cycling. Forest carbon cycle responses to interannual droughts and temperature variations in different biogeographic regions provide insights into forest function, resilience, and carbon cycling.

Drought-induced stress from water limitation in *terra firme* forests can reduce the overall capacity of the forest system to uptake atmospheric CO_2 and increase tree mortality in old growth Amazonian forests (Phillips *et al.* 2010, van der Molen *et al.* 2011) (see Section 23.1.3 in Chapter 23). Drought can directly reduce the photosynthetic capacity of forests by promoting stomatal closure (Santos *et al.* 2018, Smith *et al.* 2020, Garcia *et al.* 2021) and/or inducing leaf shedding (Doughty *et al.* 2015, Anderson *et al.* 2010), and can contribute to excess mortality. Tree vulnerability to drought, however, varies across the functional diversity of tree species, with species having more resilient hydraulic architecture (e.g., greater embolism resistance of their water-transporting xylem) less likely to succumb to drought (Rowland *et al*. 2015). This is consistent with developing ecohydrological theories of tree response to drought (Anderegg *et al*. 2018, Wu *et al.* 2020, Wang *et al.* 2020) that suggests forest vulnerability to drought is heterogeneous across the Amazon, depending on forest species composition, functional traits, and local environments (Cosme *et al.* 2017, Oliveira *et al.* 2019, Esquivel-Muelbert *et al.* 2020, Barros *et al.* 2019, Aleixo *et al.* 2019, Castro *et al.* 2020).

Declines in photosynthetic uptake and/or increases in mortality are responsible for a reduction in aboveground (Nepstad *et al*. 2004, Phillips *et al*. 2009, da Costa *et al*. 2010) and belowground biomass production (Metcalfe *et al*. 2008). In addition to the reduction in carbon assimilation by vegetation, increased tree mortality has an additive effect on the reduced capacity of Amazonian forests to assimilate and store atmospheric carbon. Droughts tend to weaken or even reverse the net Amazonian forest sink (Gatti *et al.* 2014). The net carbon sink is quantified as net biome productivity (NBP; Figure 6.1) and its reduction is the result of the additive effect of declines in photosynthesis during drought and subsequent increases in heterotrophic respiration in the following wet season (Tian *et al*. 1998, Zeng *et al*. 2008), driven by widespread drought-induced tree mortality increasing the decomposing pool (Williamson *et al*. 2000, Phillips *et al*. 2009). Droughts, such as that of 2005, can, therefore, promote biomass loss from tree mortality (approximately -1.1 [95% C.I. -2.04 to -0.49] Pg C), with an additional NPP reduction of -0.50 Pg C (Phillips *et al.* 2009). Assuming an exponential wood decomposition rate of 0.17 y^{-1} (Chambers *et al*. 2000), it is expected that annual emissions from this pool of dead wood one year after a drought account for -0.18 (95% CI from -0.32 to -0.07) Pg C, steadily reducing over time (Aragão *et al.* 2014). While it did not experience excessive drought in 2005, the central Amazon also lost biomass carbon due to blowdowns associated with a single synoptic storm event (Chambers *et al*. 2014); thus, some biomass losses attributable to climate variability can be through processes other than mortality directly related to drought stress.

Hydrologic environments significantly structure drought response; seasonally inundated floodplain forests, in contrast to *terra firme* forests discussed above, are limited by hypoxia (low oxygen) and thus droughts, rather than increasing forest stress, relieve it and induce increases in growth and NPP (Schöngart and Wittmann 2011). However, these areas are vulnerable to altered hydroperiods, as indicated by increased mortality in floodplains influenced by dams that modulate discharge and inundation (Resende *et al*. 2020). Recent studies show that even in *terra firme* forests, shallow water table regions with greater access to soil water show neutral or positive responses to drought, with decreased mortality and increases in recruitment and growth (Sousa *et al.* 2020, Esteban *et al.* 2020). Accounting for the difference between deep water table forests with limited water access, deep water table forests with large soil water storage capacity (Nepstad *et al.* 1994, Oliveira *et al.* 2005, Guan *et al.* 2015), and shallow water table forests with greater water access (one third of Amazonian *terra firme* forests) appears to reconcile earlier controversies over differences between remote sensing (which showed vegetation green up [Saleska *et al*. 2007, Brando *et al*. 2010, Samanta *et al*. 2010, Janssen *et al*. 2021]) and plot scale studies in deep water table regions (which showed negative responses to drought). An important research priority is to improve understanding of the influence of both environmental and organismal functional heterogeneities to arrive at a more integrated understanding of forest responses to environmental perturbations such as drought (Longo *et al.* 2018, Levine *et al.* 2016).

6.2.3.2 Human-Induced Fire Disturbances

Natural fires in the Amazon are rare (see Chapter 5). Human-induced land use and cover change is a major factor determining fire occurrence in Amazonian forests as they are directly related to ignition sources. Human activities associated with drou-ghts can exacerbate the occurrence of fires in the Amazon and induce their spread into adjacent forest areas, altering the carbon cycle. Old-growth forests exposed to droughts (associated with low rainfall, increases in temperature, vapor pressure deficit (VPD) inside the canopy (Ray *et al.* 2005), decreases in relative humidity (Cardoso *et al.* 2003, Sismanoglu and Setzer 2005), and decreases in plant available water (PAW) (Nepstad *et al.* 2004) are more prone to the incursion of fires related to deforestation or agricultural land management. One of the most uncertain components of Amazonian forest fire impacts is the magnitude of short- and long-term carbon emissions, potential implications for CO_2 levels in the atmosphere, and consequent global warming. Quantification of carbon emissions from understory forest fires is still lacking, preventing accurate estimates of the contribution of this component. Van der Werf *et al.* (2010)

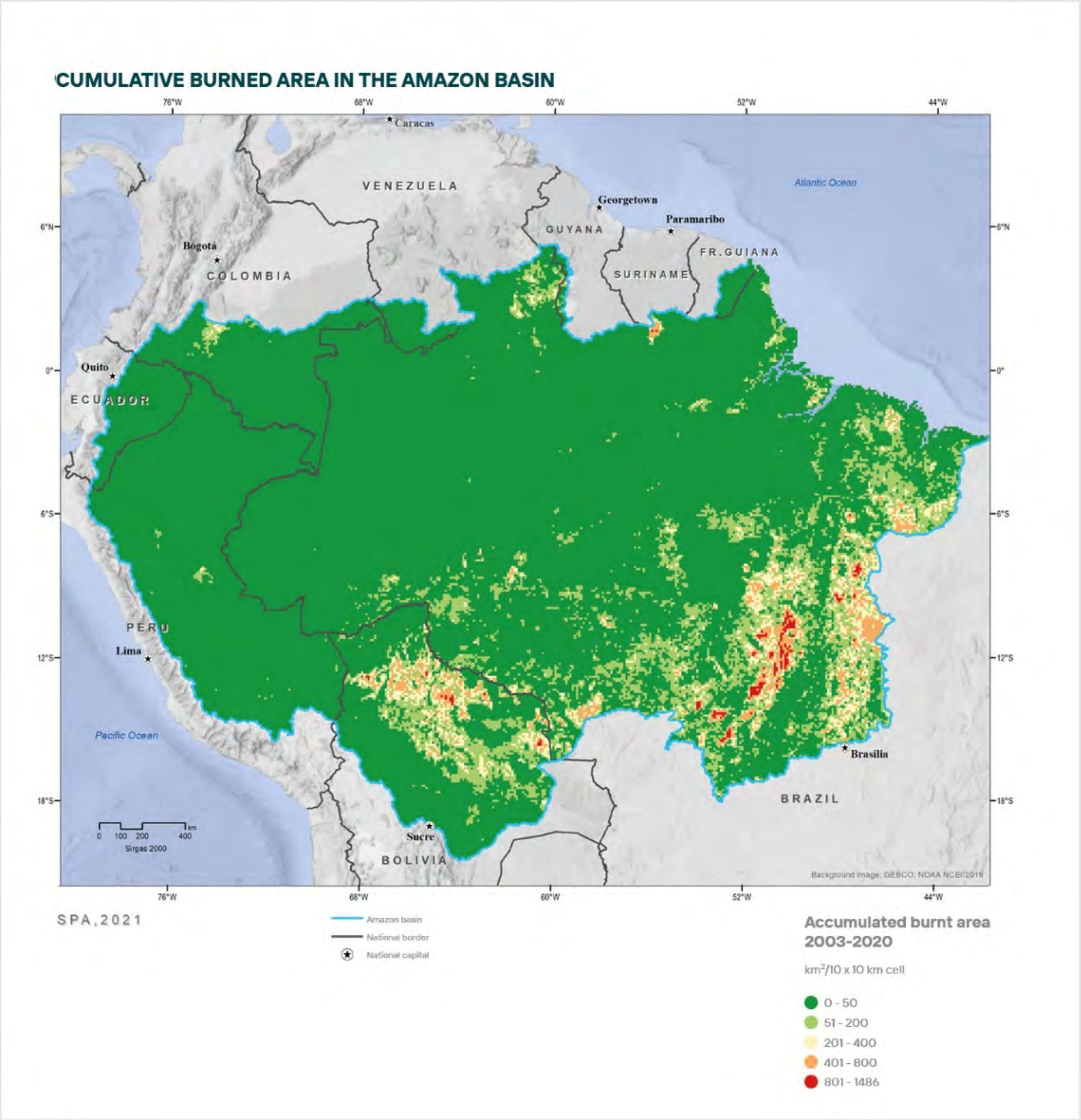

Figure 6.5. Spatial distribution of the cumulative burned area in the Amazon basin from 2003 to 2020 based on the MODIS MCD64A1 C6 product.

estimated for the period between 1997 to 2009 that globally fires were responsible for an annual mean carbon emission of 2.0 Pg C y^{-1}, with South America contributing 14.5%. Of this, about 8% appears to have been associated with forest fires, based on estimates from the Global Fire Emission Dataset (GFED) for South America. According to Silva *et al.* (2020), forest fires contribute cumulative gross emissions of carbon of ~126 Mg CO_2 ha^{-1} for 30 years after a fire event and a mean annual eflux of 4.2 Mg CO_2 ha^{-1} y^{-1}. This same study showed that cumulative CO_2 uptake of burned forests offsets only 35% (45.0 Mg CO_2 ha^{-1}) of the total gross emissions from forest fires within the same timeframe. Emissions from the decomposition of the dead organic matter account for ca. 58% (47.4 Mg CO_2 ha^{-1}) of total net emissions (Silva *et al.* 2020). The total contribution to the basin will depend on the burned area which can vary widely between drought and non-drought years. In the Brazilian Amazon between 2008 and 2012 an average of 7,800 km^2 of old-growth forest were affected by fires, with a peak of 25,400 km^2 during the 2010 drought (Aragão *et al.* 2018). For the whole Amazon, data from MODIS MCD64A1 C6 (Figure 6.5) demonstrate that an area of about 151,412±62,253 km^2 (mean±sd) km^2 $year^{-1}$ has burned in the last 18 years. It also suggests that, within this period, c.a. 60,000 km^2 of burned area occurred in areas already deforested and in areas mapped as primary forests in the year 2000 (Aragão *et al.* 2014). Forest fires result from the leakage of fires from deforested areas to adjacent forests (Aragão *et al.* 2016). Apart from at the driest fringes, most of the Amazon region is not naturally fire susceptible and its ecosystems are not resilient to fires.

6.2.4 Carbon Cycle Processes in Aquatic Amazonian Ecosystems

The uptake, release, and transport of carbon by aquatic Amazonian ecosystems is a significant component of the regional carbon cycle. High rates of primary production by plants and algae in aquatic environments, considerable sedimentation in lakes and reservoirs, and large amounts of carbon dioxide and methane emitted from rivers, lakes, and wetlands all lead to fluxes disproportionately large relative to the area of aquatic systems (Melack *et al.* 2009, Melack 2016). Remote sensing analyses of inundation and wetland habitats, inundation modeling, and extensive and intensive measurements in rivers, reservoirs, lakes, and wetlands are now available, but considerable uncertainty and information gaps remain given the diverse aquatic habitats throughout the Amazon Basin. Aquatic habitats range from headwater streams to lakes and floodplains fringing rivers. Junk *et al.* (2011) delineated major types of wetlands in the lowland Amazon based on climate, hydrology, water chemistry, and botany. Hess *et al.* (2015) used synthetic aperture radar (SAR) data at 100 m resolution to determine inundated area and areal extent of major aquatic habitats (open water, herbaceous plants, and flooded forests) within the lowland basin (<500 m). The amplitude, duration, and frequency of inundation determine the temporal and spatial variations of these aquatic habitats and associated fluxes. Multi-year time series of inundation at 0.25° resolution, and recently at 0.5 to 1 km resolution, derived from several satellite-borne sensors, are available (Hamilton *et al.* 2002, Prigent *et al.* 2020, Parrens *et al.* 2019). Hydrological models (e.g., Coe *et al.* 2007, Paiva *et al.* 2013) calculate river discharges well, while a paucity of digital elevation models on floodplains compromises inundation estimates.

Exchange of carbon dioxide and methane between surface water and the overlying atmosphere depends on the concentration gradient between air and water and on physical processes at the interface, usually parameterized as gas transfer velocity (*k*). Methane can also exit via bubbles and pass through the tissues of rooted aquatic plants, both herbaceous and woody. Water to atmosphere fluxes of carbon dioxide from all aquatic environments in the catchments of the Amazon and Tocantins river systems, covering approximately 970,500 km^2, are estimated to be approximately 722 Tg C y^{-1} (where Tg is 10^{12} grams) (Table 6.1).

Fluxes from hydroelectric reservoirs add 8.85 Tg C y^{-1}. Of the total, excluding hydroelectric reservoirs, fluxes from river channels represent about 19%, streams about 14%, floodable forests 36%, and other wetlands plus a small contribution from the open water of lakes and reservoirs about 30%. While terrestrial sources of dissolved organic carbon (DOC) and particulate organic carbon (POC) contribute to these fluxes, the majority of the carbon released to the atmosphere is likely derived from organic matter in aquatic plants photosynthesizing with atmospheric CO_2 (Mela-ck and Engle 2009). Hence, most of these water-to atmosphere fluxes represent respiration of carbon fixed within aquatic habitats, not carbon transported from uplands. To estimate net fluxes from aquatic habitats, a portion of the aquatic NPP must be subtracted from the total fluxes listed in Table 6.1.

Floodplains and other wetlands are productive aquatic environments that export considerable amounts of carbon to rivers, accumulate sediments, and provide a portion of the organic carbon that leads to the evasion of CO_2 and CH_4 to the atmosphere. Melack *et al.* (2009) summarized estimates of net primary productivity (NPP) for the plants and algae on central Amazon floodplains. The total net production attributed to flooded forests (excluding wood increments), aquatic macrophytes, phytoplankton, and periphyton within the 1.77 million km^2 portion of the Basin characterized by Hess *et al.* (2003) is about 300 Tg C y^{-1}. Flooded forests account for 62% of the total, aquatic macrophytes 34%, and the remaining 4% is associated with periphyton and phytoplankton.

Approximately 10% of the total value equals the export of organic carbon by the Amazon River (Richey *et al.* 1990), methane emission is about 2.5% (Melack *et al.* 2004) and a similar percent is likely to be buried in sediments. The remaining portion is close to being sufficient to fuel the respiration that results in the degassing of 210 ± 60 Tg C y^{-1} as carbon dioxide from rivers and floodplains for this region (Richey *et al.* 2002).

Extrapolating the estimates of aquatic NPP to the whole Amazon Basin is quite difficult. Primary production of these wetlands varies considerably between wetland types and regions from the most productive white-water river floodplains with high amounts of fertile sediments to clearwater floodplains with intermediate fertility, and black-water rivers with low fertility (Junk *et al.* 2011, Fonseca *et al.* 2019). Large uncertainties stem from the sparseness of measurements and uncertainties in habitat areas. Particularly large data gaps exist for the Llanos de Moxos (Bolivia), peatlands in the Pastaza Marañon foreland basin (Peru, Lähteenoja *et al.* 2012) and central-west Amazon (Lähteenoja *et al.* 2013), coastal freshwater wetlands (Castello *et al.* 2013), riparian zones along streams throughout the basin (Junk *et al.* 2011), small reservoirs associated with agriculture (Macedo *et al.* 2013) and habitats above 500 m. Improved estimates also require incorporation of seasonal and interannual variations in inundation and habitat areas.

Streams and small rivers likely receive almost all the CO_2 released from terrestrial-derived respiration in soils and respiration of organic C from riparian and upland litter as summarized in Richey *et al.* (2009). Inorganic and organic carbon in large rivers is provided by a combination of terrestrial and aquatic carbon sources (with the proportion unknown), and much of this organic carbon is metabolized in rivers (Mayorga *et al.* 2005; Ellis *et al.* 2012; Ward *et al.* 2013, 2016). Photo-oxidation of organic carbon appears to make small contributions to CO_2 in large rivers (Amaral *et al.* 2013, Remington *et al.* 2011).

6.3 Nutrient Cycling in the Amazon Basin

"Nutrient limitation lies at the heart of ecosystem ecology" (Townsend *et al.* 2011). Tropical forests are responsible for about a quarter of global terrestrial NPP, which, in turn, is modulated by the environmental availability of water, energy, and nutrients. Nevertheless, multiple interactions among biogeochemical cycles in multiple nutrients can affect the Amazon C cycle; co-limitation by nitrogen and phosphorus is an important constraint to plant productivity in this system. In general, weathered tropical soils have lower P availability, leading to higher N:P ratios in leaves from tropical forests when compared to high-latitude plants. In contrast, highlighting the diversity of the Amazon

Table 6.1. Annual carbon dioxide fluxes to the atmosphere from aquatic habitats in the Amazon basin including deltaic river channels, coastal freshwater habitats, and Tocantins basin. Basin areas are based on catchment boundaries for river systems, not presence of tropical forest vegetation**.** (These effluxes derive mostly from respiration of carbon produced within aquatic habitats; net fluxes require accounting for hard-to-quantify inputs from aquatic NPP).

Aquatic Habitats	Annual Carbon Dioxide Fluxes
Rivers[1]	137 Tg C y^{-1}
Streams[2]	100 Tg C y^{-1}
Lakes[3]	25 Tg C y^{-1}
Flooded forests[4]	260 Tg C y^{-1}
Other wetlands[5]	200 Tg C y^{-1}
Hydroelectric reservoirs[6]	8.85 Tg C y^{-1}

[1] Channel areas from Allen and Pavelsky (2018) plus L. Hess (personal communication) and Castello *et al*. (2013) for delta, and Sawakuchi *et al*. (2017) for Xingu and Tapajos mouthbays. Fluxes averaged from Richey *et al*. (1990), Rasera *et al*. (2008), Sawakuchi *et al*. (2017), Less *et al*. (2018) and Amaral *et al*. (2019).

[2] Johnson *et al*. (2008) approximated evasion of CO_2 from headwater streams basin wide with a statistical approach that requires validation based on actual measurements in Andean, blackwater and savanna streams.

[3] Open water area of lakes is the difference between total open water area (Hess *et al.*2015) and river channel area (Allen and Pavelsky 2018) guided by lake areas estimated by Sippel *et al*. (1992). Area includes estimates of fringing floating plants. Fluxes averaged from Rudorff *et al*. (2011), Amaral (2017) and Amaral *et al*. (2019).

[4] Floodable forests estimated by Hess *et al*. (2015), and seasonally weighted fluxes derived from Amaral *et al*. (2020).

[5] Aquatic categories lumped as other wetlands (195,000 km^2) include interfluvial wetlands in Negro basin (21,000 km^2), savanna floodplains in Roraima (4,000 km^2), Moxos (35,000 km^2) and Bananal and others in Tocantins basin (35,000 km^2), Marajos Island and other freshwater coastal wetlands (50,000 km^2), and other wetlands scattered throughout the basin (50,000 km^2). Floodable areas from Hess *et al*. (2015), seasonal averages for Roraima, Moxos and Bananal and others in Tocantins basin from Hamilton *et al*. (2002) and Castello *et al*. (2013) plus L. Hess (personal communication). Fluxes for interfluvial wetlands in Negro basin (0.77 Gg C km^{-2} y^{-1}; Belger *et al*. 2011), Roraima (3.5 Gg C km^{-2} y^{-1}; Jati 2014), Pantanal (as surrogate for herbaceous areas in Moxos, Bananal and other wetlands in Tocantins basin; 1 Gg C km^{-2} y^{-1}; Hamilton *et al*. 1995) and estimate for Marajos Island, other freshwater coastal wetlands, and other scattered inundated areas (1 Gg C km^{-2} y^{-1}).

[6] The 159 hydroelectric reservoirs currently in the Amazon basin cover approximately 5350 km^2 (Almeida *et al*. 2019). Hydroelectric reservoirs in the Tocantins basin cover approximately 5,380 km^2. Many are small and the few large ones account for most of the area. In Bolivia (50 km^2), Ecuador (35 km^2) and Peru (103 km^2) almost all are above 1,000 m asl. All in Brazil are in lowlands (<~500 masl; 10,730 km^2) with several in tropical forests and many others in tropical savannas and agricultural landscapes. Very few have adequate sampling to characterize CO_2 emissions. In contrast to methane, almost all evasion to the atmosphere occurs from the reservoir surface with little degassed at the turbines, though some CO_2 generated in the reservoir is emitted downstream (Kemenes *et al*. 2016). The estimation of emissions from Brazilian reservoirs was done in two parts: Average fluxes and areas (total 4,615 km^2) from Kemenes *et al*. (2011) plus slight additional downstream fluxes (Kemenes *et al*. 2016) for Balbina, Samuel, Curua-Una and Tucurui were used to yield 5.7 Tg C y^{-1}. The average value for Amazon reservoirs of 510 g m^{-2} y^{-1}, approximated from Barros *et al*. (2011) was applied to the remaining 6115 km^2 of Brazilian reservoirs to yield 3.1 Tg C y^{-1}. Estimating the emissions from the reservoirs in Bolivia, Ecuador the Peru is more difficult because no measurements exist and at higher elevations temperatures will be lower and the watersheds different from conditions in Brazil. Hence, half the rate applied to the southern Brazilian reservoirs is used to yield an emission of 0.5 Tg C y^{-1}. In total, emissions from hydroelectric reservoirs can be estimated to be approximately 8.85 Tg C y^{-1} with considerable uncertainty and a definite need for many more measurements, especially because more dams are planned. The extent that this estimate represents net emissions, i.e., emissions additional to those associated with the undammed rivers are unknown, but reservoir emissions are likely to be much higher than those in natural rivers.

region, less weathered soils contain a low N:P ratio, potentially making them more limited by nitrogen than by phosphorus (Nardoto *et al.* 2013). Due to the dominance of more weathered soils in the region, model results suggest that taking into account phosphorus limitation may result in a reduction in the NPP response to the increase of CO_2 in the atmosphere (CO_2 fertilization) by up to 50% in the Amazon (Fleischer *et al.* 2019).

6.3.1 Nitrogen

Nitrogen is abundant in Earth's atmosphere in the form of the N_2 molecule, but this stable form is not directly available for biological processes. The conversion of N_2 into reactive forms (e.g., NH_3, NO_X, among others) is essential for life as nitrogen is the foundation for required compounds such as proteins, enzymes, and aminoacids. Within natural ecosystems this conversion is performed by biological nitrogen fixation and, to a much smaller extent, by lightning. Another key process for life and biological functioning is the conversion of organic nitrogen into mineral forms, which are preferable to plants (ammonium [NH_4^+] and nitrate [NO_3^-]). This process, called nitrogen mineralization, is a vital part of soil fertility, and key in terrestrial tropical systems considering the high intensity of organic matter decomposition. Mineralization also leads to N immobilization, when N is incorporated in soil microbial biomass, and to denitrification, the reduction of nitrate (NO_3^-) or nitrite (NO_2^-) into the gases nitric oxide (NO), nitrous oxide (N_2O), or dinitrogen (N_2), with ensuing loss of nitrogen from the ecosystem. Inputs of nitrogen to the Amazon are derived largely from biological nitrogen fixation by microorganisms, which is a process mediated by microorganisms in symbiotic association to specific families of plants and as free-living microorganisms. Other inputs derived from atmospheric deposition are relevant in specific areas of the region.

The abundance of the Fabaceae family in the Amazon forest could indicate the important input of nitrogen through the biological nitrogen fixation (BNF). Some calculations suggested N_2 fixation on the order of 15 kg N $ha^{-1}y^{-1}$ for ecosystems on Ultisols and Oxisols, and 25 kg N $ha^{-1}y^{-1}$ in more fertile soils (Martinelli *et al.* 2012). However, Nardoto *et al.* (2012) suggested through ^{15}N analysis a low incidence of N_2 fixation by Fabaceae, and the maximum symbiotic fixation rate at the level of 3 kg N $ha^{-1}y^{-1}$ for the Amazon forest. Recent results by Reis *et al.* (2020) suggested BNF rates in South American humid forests are on the order of 10 ± 1 kg N $ha^{-1}y^{-1}$, where 60% of this total originates from free-living N fixing organisms, and 40% from symbiotic association with legume family plants. These numbers highlight the importance of internal cycling for nitrogen in the Amazon, which is strongly dependent on regular precipitation and soil water availability in the dry season and on the availability of other soil nutrients like phosphorus. Atmospheric wet and dry deposition of reactive nitrogen was estimated to be on the order of 4% of the BNF for the evergreen broadleaf forest in the Amazon (Chen *et al.* 2010). In regions under higher anthropogenic pressure, the rate of reactive nitrogen deposition can be significant; Markewiks *et al.* (2004) found that in Paragominas the N input from precipitation was on the order of 4 kg N $ha^{-1}y^{-1}$. Internal nitrogen recycling in soil, from undisturbed forests, is the main source of NO and N_2O (see Section 6.4.2) in the Amazon's atmosphere. NO emissions were measured as 4.7 ng N $m^{-2}s^{-1}$ in May 1999 (transition season) and about 4.0 ng N $m^{-2}s^{-1}$ in September 1999 (dry season) in an Amazonian rainforest site in Rondônia (Gut *et al.* 2002a). Davidson *et al.* (2008), analyzing emissions from a water-exclusion experiment in the Tapajós forest in Santarém, reported NO emissions from the control plot (an area without water exclusion) at rates of 0.9 kg N ha^{-1}, as a mean value over five years. However, these emissions do not directly reach the atmosphere above the forest. Some NO is processed within the canopy by oxidation to NO_2 and taken up by plants. Thus, there is a "canopy reduction factor" for NO_X release into the atmosphere (Gut *et al.* 2002b). These ratios can be changed in polluted air from biomass burning, which leads to high NO_X concentrations. Due to the precursor properties of NO_X molecules, ozone (O_3) concentrations also increase. NO_2 concentrations in a rainforest in Rondônia were about three times higher in September/October 1999 then during the wet season in April/May 1999 due to anthropogenic forest fires (Andreae *et al.* 2002). Enhanced NO_X concentrations lead to higher OH concentrations. As OH is the major atmospheric oxidizer, this also strongly affects the oxidation capacity of the atmosphere, which can affect rates of CCN production, cloud formation, and rainfall patterns (Liu *et al.* 2018).

Deforestation and forest regrowth affect soil nutrient cycling and nitrogen dynamics (Figueiredo *et al.* 2019). Chronosequence studies have shown enhanced gross nitrogen mineralization in young regrowing forests followed by a decay which leads to only about half the gross nitrogen mineralization in older regrowth forests compared to the undisturbed forest (Figueiredo *et al.* 2019). Further discussion on secondary forest and land use after deforestation can be found in Chapter 19.

6.3.2 Phosphorus

On the old, weathered soils found in much of the Amazon, it is likely that phosphorus is a more critical limiting macronutrient than nitrogen. Phosphorus plays an essential role in many biological processes such as metabolism and is a building block of DNA, but in natural ecosystems can be very limited. This is primarily because soluble forms of P are found at low concentrations (Markewitz *et al.* 2004, Johnson *et al.* 2001) and gaseous forms are almost non-existent (phosphine [PH_3] being a very rare exception). The effect of low P availability is further exacerbated because many tropical soils can occlude soil P and render it unavailable to plants. The main inputs of P into Amazonian ecosystems are from (i) weathering, either from local soils or from Andean material transported in rivers and deposited in floodplains, and (ii) deposition in the form of dust (e.g., from the Sahara) or ash (from biomass burning). P in biogenic aerosols and from biomass burning represents recycling of P largely within the Amazon system, whereas P deposition from Saharan dust represents a new atmospheric input of P.

The main loss term is export of sediment or organic material via river systems, or through harvesting. Within the basin, lateral movement of P, for example from floodplains rich in Andes-derived sediments, may be facilitated by animals (Doughty *et al.* 2013, Buendía *et al.* 2018); such animal-mediated lateral transfer may have been much stronger in the past prior to megafaunal extinction and more recent defaunation. Total atmospheric deposition of P is estimated to be 16–30 kg P km^{-2} y^{-1} (Vitousek and Sanford 1986), of which Saharan dust inputs are estimated to be no more than 13%, and the bulk is from biogenic aerosols and biomass burning (Mahowald *et al.* 2005). Vitousek and Sanford (1986) estimated that the recycling of phosphorus through litterfall is 140–410 kg P km^{-2} y^{-1}, an order of magnitude greater than atmospheric inputs.

Local weathering inputs are estimated to average 2.5 kg P km^{-2} y^{-1} (Doughty *et al.* 2013). However, weathering rates are variable, and the oxisols that dominate much of the eastern Amazon have virtually no weatherable appatite left, so weathering inputs of P are practically zero. The Amazon Basin experiences continental isostatic rebound, where the slow erosion rates are compensated by slow uplift and weathering of new material (Buendía *et al.* 2018). For the area of the Amazon Basin (including the Guyanas), total P inputs are ~2.8 Tg C y^{-1}. Fluvial export of P, based on discharge at Óbidos, is 1.46 Tg P y^{-1}, about half of the inputs to the basin (Devol *et al.* 1991).

There are strong gradients in P availability across the basin, with the lowest availability on old, weathered oxisols of the eastern Amazon, and higher concentrations on younger soils in the western Amazon (Aragão *et al.* 2009, Quesada *et al.* 2010). The high productivity of the Amazon forest, despite this low P availability, is facilitated by very tight recycling of P within the forest system, where around half of leaf P is either resorbed prior to leaf senescence, and most of the rest is rapidly captured by fungal hyphae soon after litter fall or plant death (Cuevas and Medina 1986, Markewitz *et al.* 2004).

6.4 Other Major Greenhouse Gases

6.4.1 Methane

6.4.1.1. Terrestrial Methane Fluxes

Methane is a strong greenhouse gas due its importance in radiative forcing, contributing to climate change and with a warming potential relative to CO_2 of 28-34 for a 100-year time horizon. In addition, methane is the primary anthropogenic volatile organic compound (VOC) in the global troposphere (Fiore *et al.* 2002), contributing to tropospheric O_3 formation by photochemical reactions (West *et al.* 2006). In the stratosphere, methane reacts with chlorine atoms, which is a stratospheric ozone-depleter (Cicerone 1987). Methane is produced by different processes (i.e., biogenic, thermogenic, or pyrogenic), can be of anthropogenic or natural origin, and is consumed by a few sinks. The balance between sources and sinks determines the methane budget. In terrestrial environments, anoxia in soil leads to the production of methane as a terminal step in the degradation of organic matter by anaerobic methanogenic archaea. Methanotrophs in terrestrial soils can consume methane under aerobic conditions. The balance between the two processes is regulated by climatic and edaphic factors, such as soil temperature, oxygen content, soil pH, water table, and electron acceptors (Conrad 2009).

Well-drained soils of the Amazonian upland forest are often a net CH_4 sink, estimated to be 1-3 Tg CH_4 y^{-1} (Davidson and Artaxo 2004, Dutaur and Verchot 2007). However, rainfall, poor drainage, and soil properties can create localized anoxic microsites that can facilitate methane production, causing forests to switch from sinks to small sources (Verchot *et al.* 2000). Oxygen availability in forest soils is known to influence methane production, with emissions of 0.5-2.3 mg of CH_4 $m^{-2}d^{-1}$ observed in a montane forest in Puerto Rico (Teh *et al.* 2005). Anaerobic decay of waterlogged wood (Zeikus and Ward 1974) and deadwood (Covey *et al.* 2016) are also sources of methane. Methane can be produced by a variety of fungi and archaea within tree stems, a process identified by Zeikus and Ward (1974) and now recognized as common and perhaps present in living trees with no visual decay (Covey & Megonigal 2018).

Methane sources have been detected within forest canopies (Carmo *et al.* 2006). Tank bromeliads (Martinson *et al.* 2010) and termites (Martius *et al.* 1993) are known to produce methane and also harbor methanogens. Large, site specific emissions from termites (25.9 ± 11.2 mg CH_4 g termite^{-1} y^{-1}; Martius *et al.* 1993) and tank bromeliads (3.6 g CH_4 ha^{-1} d^{-1}; Ecuadorian Andes, Martinson *et al.* 2010) have been reported. A recent study in the Amazon found high emissions from mounds of soil feeding termites ranging from 3.5-16.4 µg CH_4 m^{-2} d^{-1}, suggesting the role of termites is likely underestimated at an ecosystems scale (van Asperen *et al.* 2020). Epiphytic bryophytes on tree stems and branches can act as sources and sinks of methane, as indicated by two studies in non-Amazonian forests (Lenhart *et al.* 2015, Machacova *et al.* 2017). These methane sources within canopies are highly heterogeneous with limited measurements, hence, it is difficult to estimate their regional strength.

Methane can be produced by a novel abiotic pathway from plant tissues, with an estimated global source strength of up to 1 Tg CH_4 y^{-1} (Bloom *et al.* 2010). Reactive oxygen species in plant tissues commonly produced in response to plant stress are known to drive these abiotic methane emissions. Upland tree stem and leaf surfaces are postulated to offer additional terrestrial sinks (Covey and Megonigal 2018); however, direct observations are presently lacking.

Anthropogenic activities in terrestrial ecosystems can both emit or take up methane. Briefly, land use changes such as logging or conversion of forests to agriculture reduce the capacity of the soil methane sink due to soil compaction (Bustamante *et al.* 2009). Forest fire is known to emit methane in the short term (Wilson *et al.* 2016), reduce the methane sink in some forests, and reduce methane emissions from wetland trees in flooded forests initially, but later may result in enhanced emissions due to the increased availability of substrates for methanogenesis. Land conversion to animal farming with the introduction of ruminant livestock increases emissions due to enteric fermentation. Waste management and direct production during biomass burning increases methane emissions. Land conversion following river damming changes the flooding regime both upstream and downstream and are documented to increase methane emissions (see next section).

6.4.1.2. Freshwater Methane Fluxes

Methane emission to the atmosphere from aquatic environments (Table 6.2) reflects differences between CH_4 production by methanogens, mainly in anoxic sediments, and consumption by methanotrophs, as well as physical processes. These processes are influenced by environmental variables such as water temperature, dissolved oxygen, trophic status, and substrate availability. CH_4 can reach the atmosphere by three pathways: via diffusive fluxes at the air-water interface; via bubbles that form in the sediment, rise through the water column, and are emitted to the atmosphere (ebullition); and through the vascular systems of herbaceous and woody plants. Wetland-adapted trees are known to transport and emit soil-produced methane to the atmosphere via tree trunk and leaf surfaces (Pangala *et al.* 2017). Ebullitive fluxes depend on bubble formation and hydrostatic pressure over the sediment, while diffusive fluxes are dependent on concentration gradients and turbulence, which vary on multiple time and spatial scales. Factors such as wind speed, diel variation in thermal structure, and physical processes such as convective and advective mixing are all known to influence gas distributions and transfer velocities, and consequently gas fluxes.

Table 2 summarizes methane fluxes from major aquatic environments in the Amazon Basin. Fluxes of methane from all aquatic environments within the catchments of the Amazon and Tocantins river systems, covering 970,500 km^2, are estimated to be approximately 51 Tg CH_4 y^{-1}. Given the varied approaches and associated uncertainties in these values, the procedure used for each category is described briefly – including both the area of each category and the average annual flux per km^2, based on selected studies with the most comprehensive or representative data, where possible.

River channel areas (85,500 km^2) are based on Allen and Pavelsky (2018) plus L. Hess (personal communication) and Castello *et al.* (2013) for the delta, and Sawakuchi *et al.* (2017) for the Xingu and Tapajos mouthbays. Average fluxes (8 Mg CH_4 km^{-2} y^{-1}) are from Sawakuchi *et al.* (2014) and Barbosa *et al.* (2016). Stream channel area (50,000 km^2) is estimated from geomorphological features (Richey *et al.* 2002, Beighley and Gummadi 2001), and average fluxes (6.6 Mg CH_4 km^{-2} y^{-1}) for tropical and subtropical streams are from Stanley *et al.* (2016). Open water area of lakes is the difference between total open water area (Hess *et al.* 2015) and river channel area (Allen & Pavelsky 2018) guided by lake area estimates by Sippel *et al.* (1992). Lake area includes estimates of areas with floating plants. Fluxes are averaged from Barbosa *et al.* (2020). Floodable forest area (615,000 km^2) is derived from Melack & Hess (2010) and Hess *et al.* (2015). Seasonally weighted fluxes from water surfaces under flooded forests (26.6 Mg CH_4 km^{-2} y^{-1}) are derived from Barbosa *et al.* (2020), Barbosa *et al.* (2021) for *várzea*, and from Rosenqvist *et al.* (2002) for *igapó*. Fluxes through trees in flooded forests are estimated to be 21.2 ± 2.5 Tg CH_4 y^{-1}; forested wetland soils are responsible for an additional 1.1 ± 0.7 Tg CH_4 y^{-1} (Pangala *et al.* 2017).

Aquatic categories lumped as other wetlands (195,000 km^2) include interfluvial wetlands in the Rio Negro Basin (21,000 km^2); savanna floodplains in Roraima (4,000 km^2), Moxos (35,000 km^2), Bananal, and others in the Tocantins Basin (35,000 km^2); Marajos Island and other freshwater coastal wetlands (50,000 km^2); and other wetlands scattered throughout the basin (50,000 km^2). Floodable areas are based on Hess *et al.* (2015); seasonal averages for Roraima, Moxos, Bananal, and others in the Tocantins Basin are from Hamilton *et al.* (2002) and Castello *et al.* (2013), plus L. Hess (personal communication). Fluxes are estimated as follows:

interfluvial wetlands in the Rio Negro Basin 28 Mg CH_4 km^{-2} y^{-1} (Belger *et al.* 2011), Roraima 5.3 Mg CH_4 km^{-2} y^{-1} (Jati 2014), Pantanal, as a surrogate for herbaceous areas in Moxos and elsewhere) 80 Mg CH_4 km^{-2} y^{-1} (Hamilton *et al.* 1995), and estimates for Marajos Island and other freshwater coastal wetlands (27 Mg C km^{-2} y^{-1}).

Hydroelectric reservoirs (158) in the Amazon Basin currently cover approximately 5,350 km^2 (Almeida *et al.* 2019; see footnotes in Table 6.2). Hydroelectric reservoirs in the Tocantins Basin cover approximately 5,380 km^2. Very few have adequate sampling to characterize methane emissions. One example is Balbina, where measurements over a year were made of diffusive and ebullitive fluxes from multiple stations within the reservoir, degassing at the turbines and downstream (Kemenes *et al.* 2007). Another example is the multiyear study at Petit Saut (French Guiana) that included measurements in the reservoir and downstream (Abril *et al.* 2005). Both these studies indicate the importance of degassing of methane through the turbines and downstream. Additional measurements at Tucurui, Samuel, and Curua-Una reservoirs indicated the significance of degassing at the turbines and downstream (Kemenes *et al.* 2016). Extrapolating all emissions based on reservoir areas combined with turbine and downstream emissions yields a total of 0.4 Tg CH_4 y^{-1} for Balbina, Curua-Una, Samuel, and Tucurui. To estimate emissions from the other Brazilian reservoirs, an overall average diffusive and ebullitive emission from the surfaces of ten reservoirs within southern portions of the basin (~29 g CH_4 m^{-2} y^{-1}, as summarized in Deemer *et al.* 2016) and the combined surface areas of all the additional Brazilian reservoirs yields 0.18 Tg CH_4 y^{-1}.

Estimating emissions from reservoirs in Bolivia, Ecuador, and Peru is more difficult because no measurements exist and at higher elevations temperatures will be less and the watersheds different from conditions in Brazil. Hence, half the rate applied to the southern Brazilian reservoirs is used to yield an emission of ~0.002 Tg CH_4 y^{-1}. In total, methane emissions from hydroelectric reservoirs can be estimated to be approximately 0.58 Tg CH_4 y^{-1} (Table 6.2) with considerable uncertainty and a definite need for many more measurements, including degassing through turbines and downstream, especially because more dams are planned. The extent that this estimate represents net emissions, i.e., emissions additional to those associated with the undammed rivers, are unknown, though upland forest soils are likely to be sinks for methane.

Table 6.2. Annual methane fluxes to the atmosphere from aquatic habitats in the Amazon basin including deltaic river channels, coastal freshwater habitats and Tocantins basin plus hydroelectric reservoirs.

Aquatic Habitats	Annual Methane Fluxes
Rivers	0.7 Tg CH_4 y^{-1}
Streams	0.4 Tg CH_4 y^{-1}
Lakes	0.7 Tg CH_4 y^{-1}
Flooded forests	
Flux from water surface	16.4 Tg CH_4 y^{-1}
Flux through trees	21.2 Tg CH_4 y^{-1}
Flux from exposed soil	1.1 Tg CH_4 y^{-1}
Other wetlands	9.6 Tg CH_4 y^{-1}
Hydroelectric reservoirs	0.58 Tg CH_4 y^{-1}

As noted in Section 6.2.2, large uncertainties stem from the sparseness of measurements of fluxes and uncertainties in habitat areas and their seasonal and interannual variations. Temporal differences in methane fluxes are owed to variations in inundation as a result of differences in river discharge, local runoff and rainfall, related ecological conditions, and changes in areal coverage of different habitats. Multi-year time-series of measurements are not available to document possible trends or variations. Current hydrological models provide estimates of variations in inundation, but underestimate basin-wide conditions. Remote sensing products include inundated areas, though the longest time-series under-estimate areas in some habitats and have moderate spatial resolution; high resolution products are temporally sparse. Distinguishing among the varied aquatic habitats relies on a combination of optical and microwave products which lack sufficient time-series.

6.4.1.3. Amazon Methane Budget

Both bottom up and top-down estimates with different spatial and temporal scales are available for the Amazon Basin. Bergamaschi *et al.* (2009) used SCIAMACHY data to calculate total Amazon emissions of 47.5 to 53.0 Tg CH_4 y^{-1} in 2004 for an area of 8.6 × 10^6 km^2. Based on an inversion model using *in situ* and remote sensing observations, Fraser *et al.* (2014) estimated emissions of 59.0 ± 3.1 Tg CH_4 y^{-1} from tropical South America (approximately ~9.7 × 10^6 km^2) in 2010. Tunnicliffe *et al.* (2020) using inverse modelling estimates derived from GOSAT satellite measurements combined with surface data, and the high-resolution regional atmospheric transport model NAME, reported mean emissions for wetlands in the Brazilian Amazon substantially lower than other estimates (9.2 ± 1.8 Tg CH_4 y^{-1}). Wilson *et al.* (2016) performed an inversion with the TOMCAT model using aircraft vertical profile observations and estimated methane emissions of 36.5 to 41.1 Tg CH_4 y^{-1}in 2010 and 31.6 to 38.8 Tg CH_4 y^{-1} in 2011 (area of 5.8 x 10^6 km^2), with non-combustion emissions representing 92-98% of total emissions. Pangala *et al.* (2017) provide a regional estimate of methane emissions of 42.7 ± 5.6 Tg CH_4 y^{-1} (area of 6.77 x 10^6 km^2) based on regular vertical lower troposphere profiles covering the period 2010–2013, where 10% came from biomass burning. This estimate is similar to bottom-up estimates for the same area. Estimates of total methane fluxes based on aircraft vertical profiles measurements for the northeastern Amazon (2.8°S, 54.9°W; considering an area of 0.6 x 10^6 km^2) are between 7.5 and 11.7 Tg CH_4 y^{-1} (Miller *et al.* 2007, Basso *et al.* 2016, Pangala *et al.* 2017), where natural sources, like wetlands, are likely important, with biomass burning representing almost 10% of total annual mean flux and anthropogenic emissions representing around 11% of the annual mean flux (Basso *et al.* 2016). This region has higher fluxes than other regions (Wilson *et al.* 2016, Pangala *et al.* 2017), which highlights regional variability in methane emissions in the Amazon.

The overall methane budget includes multiple sources and sinks whose contributions are sensitive to feedback from drought conditions, and significant gaps remain in understanding how droughts will affect methane budgets (Saito *et al.* 2016). During the 2010 drought, methane emissions from biomass burning were around 5-6 times higher than 2011, varying from 0.5 to 7.0 Tg CH_4 y^{-1} depending on the climate condition (drought years), which part of the Amazon was being considered, and the severity of the burn season (Wilson *et al.* 2016, Saito *et al.* 2016).

Top-down estimates of methane emissions indicate that the Amazon is an important source; extrapolating these estimates for the same area (an Amazon area of 6.77 x 10^6 km^2) total methane emissions vary between 36.9 and 48.0 Tg CH_4 y^{-1} (Bergamaschi *et al.* 2009, Fraser *et al.* 2014, Wilson *et al.* 2016, Pangala *et al.* 2017). This suggests the region contributes 6-8% of global methane emissions, considering global emissions of 576 Tg CH_4 y^{-1} (Saunois *et al.* 2020).

6.4.2 Nitrous Oxide (N_2O)

6.4.2.1 Terrestrial Biosphere N_2O Processes

Nitrous oxide (N_2O) is, after carbon dioxide (CO_2) and methane (CH_4), the third most important long-lived greenhouse gas, and one of the main stratospheric ozone depleting substances. The majority of anthropogenic N_2O is produced by the agricultural sector, although natural systems emit nitrous oxide via organic matter decomposition processes, particularly in the soil. Emissions of N_2O, predominantly from denitrification, are related to biological and physical-chemical characteristics of the soil. Soil microbial processes modulate organic matter mineralization and environmental conditions such as soil water content, N availability, soil texture, pH, and labile organic carbon content are important conditions for the transformation of organic matter and dissolved nutrients to plants and soil biota. Rapid nutrient cycling related to higher temperatures, water availability, and high N:P ratios result in tropical forests emitting high rates of N_2O to the atmosphere. Tropical regions account for 71% of global natural ecosystem emissions (Yu and Zhuang 2019). Ciais *et al.* (2014) reported global N_2O emissions from natural vegetation of 6.6 Tg N y^{-1} (ranging from 3.3 to 9.0 Tg N y^{-1}, IPCC AR5). Recently, Tian *et al.* (2020) reported global emissions from natural soils (with strong contributions from the tropics) in the period from 2007-2016 on the order of 4.9 to 6.5 TgN y^{-1}. Syakila and Kroeze (2011) simulated an increase of 8 times, of total anthropogenic N_2O emissions, from the beginning of the industrial revolution to 2006, from 1.1 TgN y^{-1}, in 1850 to 8.3 Tg N y^{-1} in 2006, with the emissions from global natural systems maintained at 10.5 Tg N y^{-1}. Over the same period, the global N_2O Model Intercomparison Project (NMIP) simulations (from 1860 onwards) indicate the highest N_2O global emissions derived from tropical areas, and tropical South America (particularly the Amazon region), accounting for 20% of global emissions (Tian *et al.* 2018). The models consider natural and human transformed land use (e.g., agriculture, pasture) in the simulations.

6.4.2.2. Freshwater Biosphere N_2O Processes

Most N_2O emissions from freshwater systems occur in wetlands. Guilhen *et al.* (2020), in a study of the wetlands along the Amazon, Madeira, and Branco rivers, circa 1.3 x 10^6 km^2, modelled N_2O emissions from denitrification on the order of 1.8 kg N_2O $ha^{-1}y^{-1}$, peaking in March. Total emissions from denitrification in the Amazon Basin floodplains are estimated to be 1.03 Tg N- N_2O y^{-1}. Due to the abundance of nitrogen in Amazonian soils, nitrate may not be limiting denitrification in the Amazon Basin (Guilhen *et al.* 2020).

6.4.2.3. The Amazon N_2O Budget

Estimates for N_2O emissions in tropical forest soils ranged from 0.8 Tg N y^{-1} (mean for 1991–2000) for South America (Felipe Pacheco and INMS, personal communication) to 2.40 Tg N y^{-1} (Matson and Vitousek 1990) and 3.55 Tg N y^{-1} (Breuer *et al.* 2000) for tropical humid forests globally. Melillo *et al.* (2001) and Davidson *et al.* (2001) calculated emissions from the Amazon tropical forest of 1.2 to 1.3 Tg N y^{-1}. Buscardo *et al.* (2016) estimated the highest N_2O emissions in the north-west portion of the basin, decreasing with drier conditions towards the east and south, with an average estimate of 0.74 to 0.83 Tg N y^{-1} for the entire Amazon Basin. Variation was due to the fraction attributed to soil respiration. Figueiredo *et al.* (2019) and Galford el al. (2010) suggest that the Amazon's mature forests (including *terra firme* and periodically flooded forests) are responsible for circa of 6.5% of global N_2O emissions from natural systems, and fluxes are estimated on the order of 0.5-2.5 kg N ha^{-1} (Lent *et al.* 2015, Tian *et al.* 2020). In a comprehensive review conducted by Meurer *et al.* (2016) it was shown that the median annual flux rates from Amazonian forests were about 36% higher than the N_2O fluxes rates from the Atlantic rainforest (2.42 and 0.88 kg N ha^{-1}, respectively). Land use change significantly alters the emissions of N_2O. Due to increased soil N availability, when pasture replaces the forest, fluxes may double or triple, but then decrease in the years following conversion to less than half of the original emissions (Davidson *et al.* 2007). Biomass burning is currently responsible for about 0.7 Tg N y^{-1} emission of N_2O (Davidson and Kanter 2014). In agricultural systems in the Amazon region, double cropping is important, with soy-maize and soy-cotton the most common rotation. Soy fixes nitrogen at a rate of 200 kg ha^{-1}, but N_2O emissions are fairly low, 0.1-0.2 kg ha^{-1} (Cruvinel *et al.* 2011). The following crop, with the addition of mineral fertilizer, emits N_2O on the order of 0.2 to 0.8 kg ha^{-1}, depending on the amount of fertilizer used (Jankowski *et al.* 2018). Regional N_2O emissions from natural ecosystems are presented in Figure 6.6.

6.5 Aerosols and Trace Gases

6.5.1 Biogenic Non-Methane Volatile Organic Compounds (NMVOCs)

The Amazonian ecosystem is regarded as the largest source of biogenic Non-Methane Volatile Organic Compounds (NMVOCs), also known as biogenic volatile organic compounds (BVOCs) (Figure 6.7). Emissions of NMVOCs make a minor contribution to the carbon cycle (Figure 6.2, Kesselmeier *et al.* 2002). Biogenic NMVOCs are characterized by their high chemical reactivities and thus represent key players in oxidation processes in the atmosphere (Williams *et al.* 2016, Nölscher *et al.* 2016, Pfannerstill *et al.* 2018). They affect atmospheric chemistry and physics in major ways, by changing the oxidation capacity and particle production, and delivering so-called secondary organic aerosols (SOA) which add to the effects of primary biological particles in the atmosphere. Anthropogenic effects as well as climate and global change have severe effects on NMVOC emission rates (Peñuelas and Staudt 2010, Liu *et al.* 2016) and affect particle production, with consequences for water condensation, cloud production, and the water cycle.

Of significance is the heterogeneity of VOC emissions from vegetation and the dynamics of seasonal or developmental changes in the Amazon (Yáñez-Serrano *et al.* 2015, 2020). With increasing understanding of biogeochemical cycles and atmospheric reactivity, there is growing interest in the large group of biogenic NMVOCs, which represent the dominant source of organic volatiles in the atmosphere, especially in forest dominated areas. Biogenic production and release of NMVOCs are closely related to plant biodiversity and, consequently, the number of biogenic volatiles is enormous (Kesselmeier and Staudt 1999, Laothawornkitkul *et al.* 2009). In line with their large numbers, their roles are still a matter of discussion in view of ecology and chemistry. In particular, the complex composition of BVOCs, including oxygenated species, aromatic compounds, sulfurous compounds, oxidation products, and further unknown reactive compounds leaves questions about atmospheric reactivity (Kesselmeier and Staudt 1999, Nölscher *et al.* 2016, Pfannerstill *et al.* 2018, Yáñez-Serrano *et al.* 2018).

NMVOC research in the Amazon. Field locations such as the Amazonian Tall Tower Observatory (ATTO) can contribute to this research (Andreae *et al.* 2015). Complications arise from deforestation, which changes the diversity of volatiles and thus chemical reactivity. The loss of forested areas will affect not only the carbon cycle but also NMVOC exchange between the surface and the atmosphere, particle production, and the water cycle. Furthermore, the influence of fires on particle numbers are impressive, when comparing the dry season (with fire) to the wet season (without fires) (Andreae 2019, Pöhlker *et al.* 2019). Conversely, direct SOA contributions from fire emissions seems to be low when analyzing Mediterranean fires (Bessagnet *et al.* 2008). Significant gaps in understanding the emission regulation and fate of emitted NMVOCs remain. Major unknowns with potential impact are the emission capacity and quality of flooded areas, the role of root anoxia (Bracho-Nunez *et al.* 2012), and ecological interactions within the forest (Salazar *et al.* 2018).

6.5.2 Physics and Chemistry of Aerosols and Cloud Condensation Nuclei (CCN)

Besides influencing water and nutrient cycles, aerosols affect radiation directly by light scattering and absorption as well as indirectly by cloud condensation and processing. Under natural conditions, the Amazon is one of the few continental regions where aerosol concentrations resemble those of the pre-industrial era, in the range of 300-500 particles per cm^3 and 9-12 $\mu g/m^3$ (Andreae 2007, Martin *et al.* 2010). Organic carbon dominates the composition of submicrometer aerosols in the Amazon in the wet season, comprising about 70% of mass, followed by sulfate (10-15%) and equivalent black carbon (5-10%) (Andreae *et al.* 2015, Chen *et al.* 2015). Observations indicate that about 90% of submicron organic aerosol mass results from secondary production (Chen *et al.* 2009). Oxidation of BVOCs by O_3 and OH leads to the formation of semivolatile organic species, with sufficiently low vapor pressure to condense over preexistent particles and produce secondary organic aerosols (SOA) (Graham *et al.* 2003, Pöhlker *et al.* 2012). Another pathway for the production of SOA from BVOC emissions consist of aqueous-phase

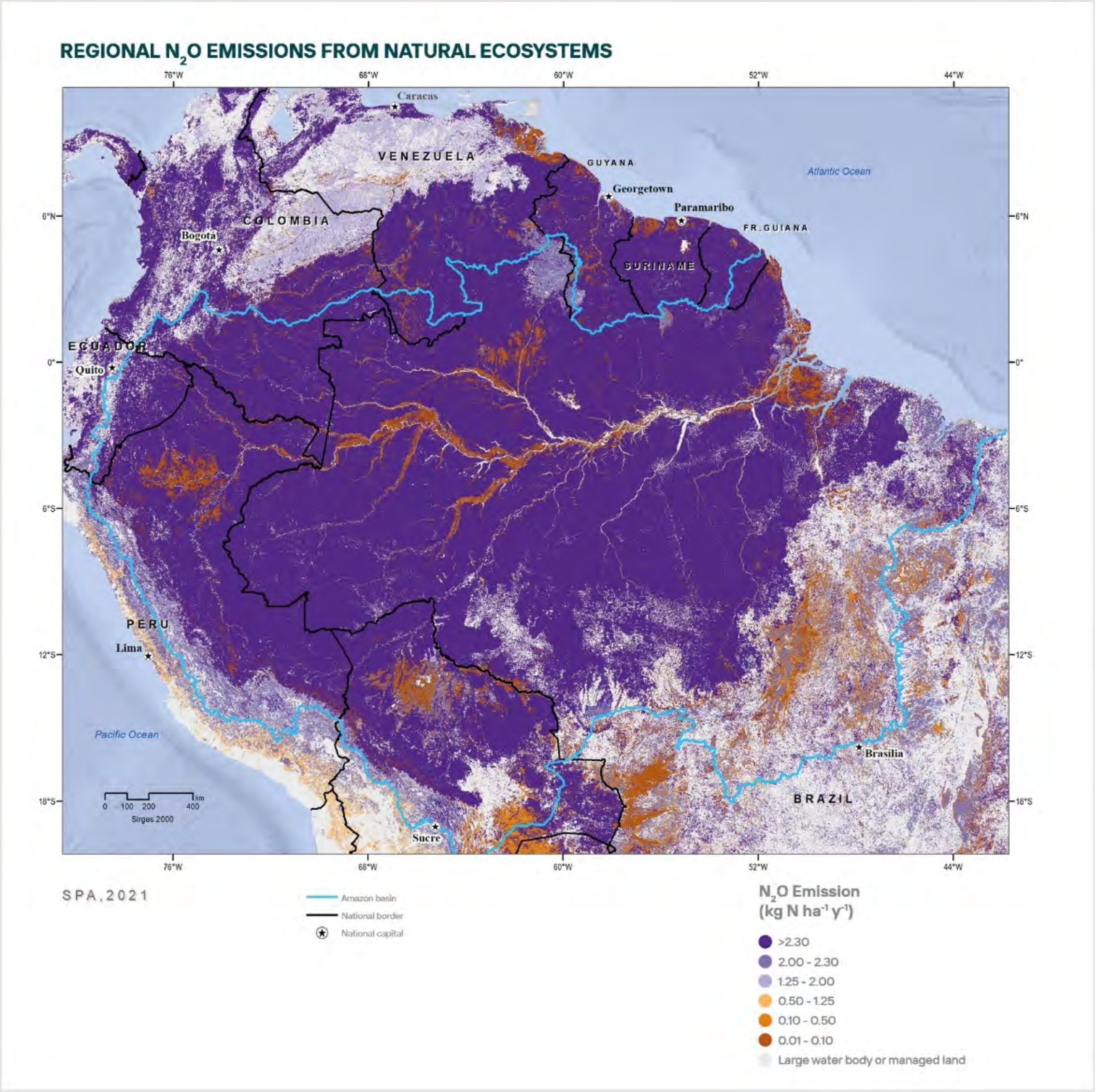

Figure 6.6 N_2O emissions in the Amazon. Data produced by Felipe Pacheco, based on data and analysis from the International Nitrogen Management Assessment (INMS).

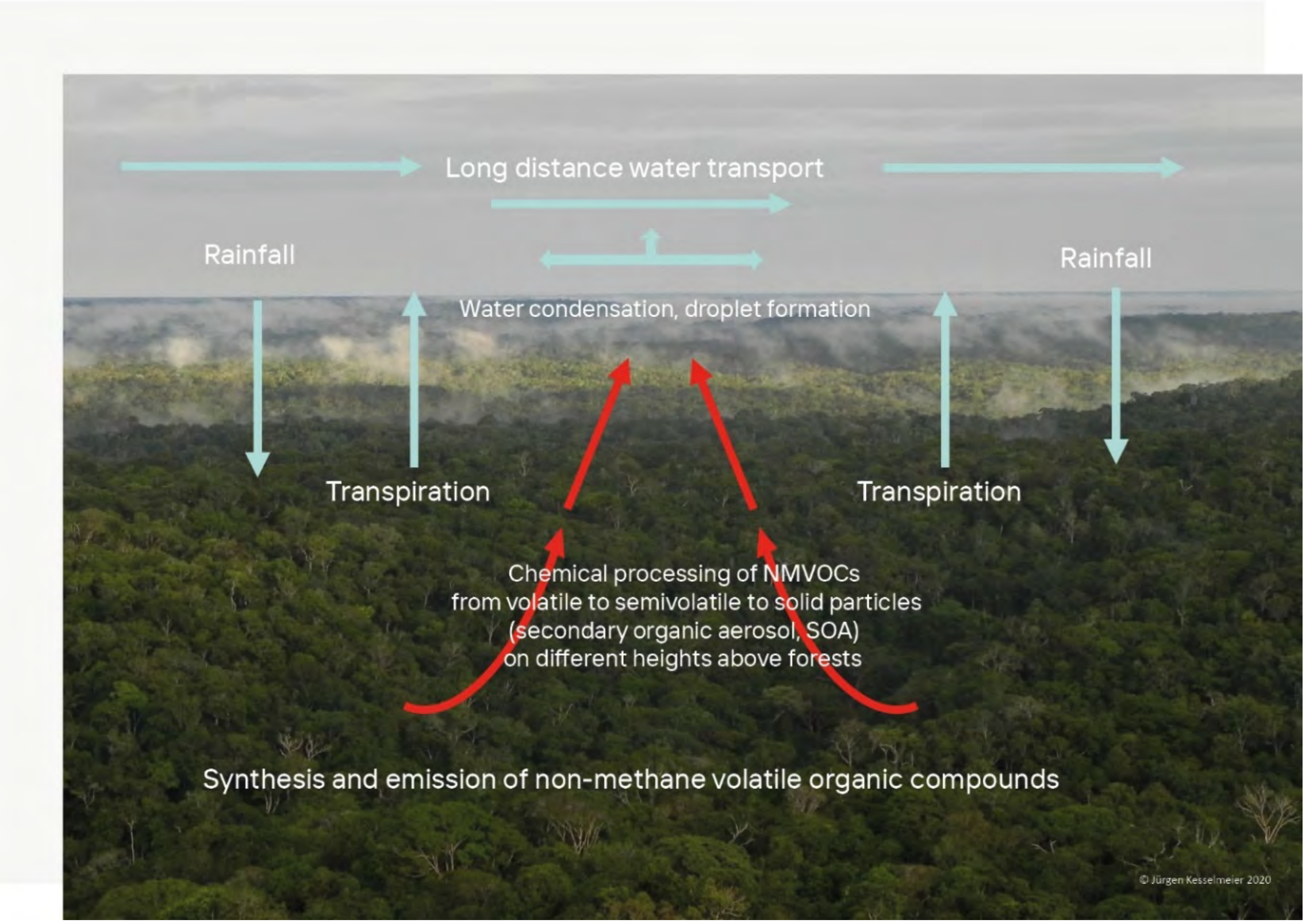

Figure 6.7 The NMVOC emissions of the Amazonian rainforest act as a water catching and water transporting organic system by chemical and physical processing of biogenic trace gases to secondary organic aerosol serving as condensation nuclei for water vapor.

oxidation and acid-catalyzed reactive uptake of isoprene oxidation products within cloud and fog droplets (Lim *et al.* 2010, Surratt *et al.* 2010). Characterization of submicrometer organic aerosols in a forest site in the Amazon suggests comparable importance of aqueous and gas-phase pathways of SOA production (Chen *et al.* 2015).

Another mechanism of SOA production is new particle formation (NPF) in the diameter range <10 nm, followed by condensational growth to the accumulation mode (~100-300 nm). This process has been demonstrated to be a relevant source of particles in boreal forests (Dal Maso *et al.* 2005). However, the impact of NMVOC on particle production over the Amazon is surprisingly different from what occurs in temperate and boreal forests (Andreae *et al.* 2018, Artaxo *et al.*, in review). Long-term observations at Amazonian forest sites have shown that regional-scale NPF events are infrequent near the surface (3% of measurement days) (Rizzo *et al.* 2018). Instead, airborne measurements in the Amazon reported high concentrations of nucleation and Aitken mode particles (diameter <~100 nm) in the upper troposphere. A conceptual model was developed to describe this important source of particles in the Amazon (Figure 6.8). BVOCs emitted at the vegetation canopy surface are transported upward inside convective clouds to the upper troposphere, where they experience the ideal conditions for particle nucleation (high actinic flux, low temperatures, and small condensation sink). SOA are

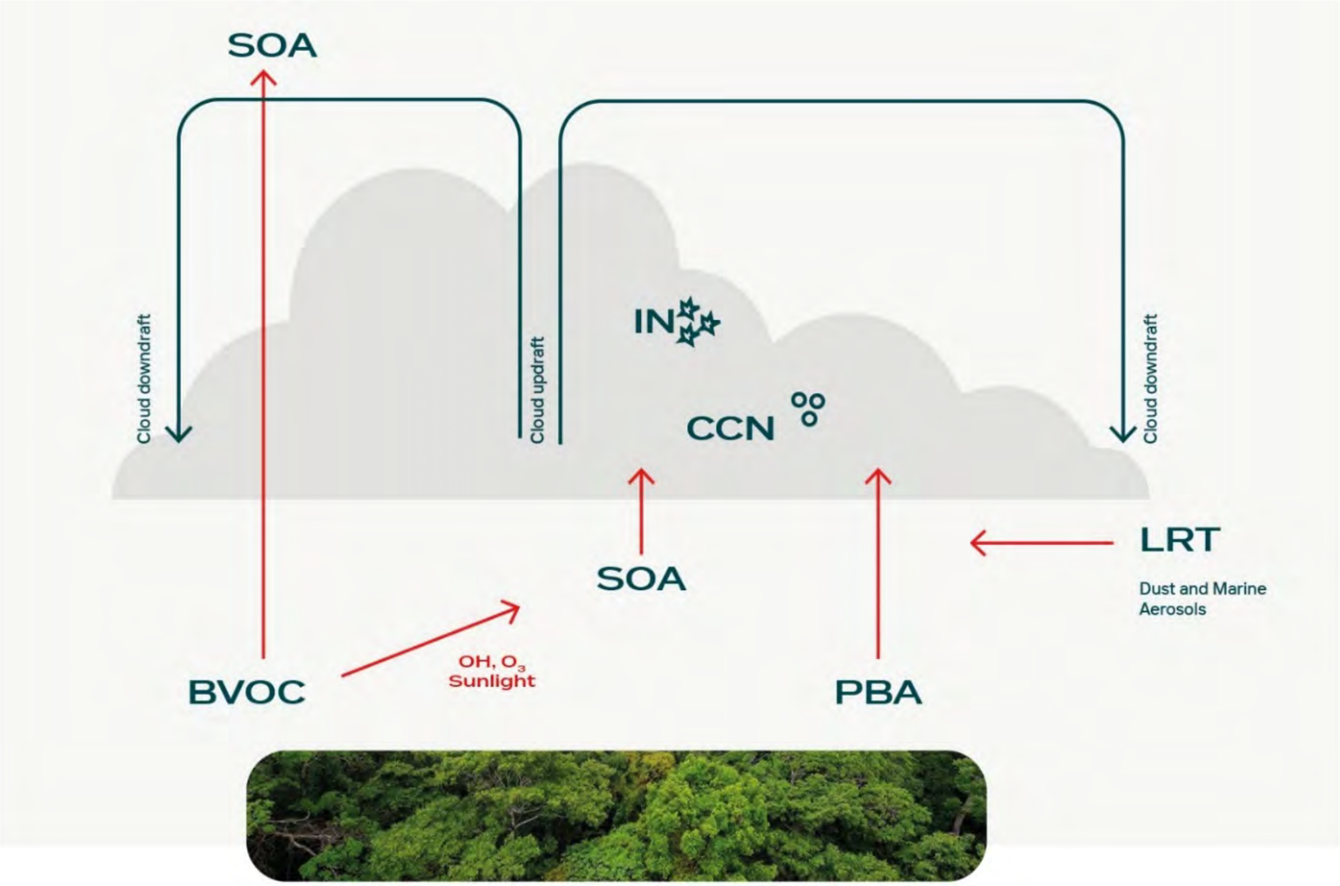

Figure 6.8. Interactions between biogenic emissions, long range transport (LRT) of aerosols and clouds in Amazon. Biogenic volatile organic compounds (BVOCs) are oxidized near the surface, leading to the production of secondary organic aerosols (SOA). Primary biological aerosols (PBA), SOA and LRT aerosols activate into cloud condensation nuclei (CCN) and ice nuclei (IN), promoting the development of clouds and precipitation. BVOCs are transported by convective updrafts to the upper troposphere, where ideal conditions for particle nucleation are found. SOA are produced from BVOC oxidation in the upper troposphere and are eventually transported to the surface by convective downdrafts, constituting an important natural source of particles.

produced from BVOC oxidation in the upper troposphere and are eventually transported to the surface by convective downdrafts, increasing in size by condensation on the way down (Andreae *et al.* 2018, Wang *et al.* 2016).

In the Amazon forest, coarse mode aerosols (diameter >2.5 µm) dominate the mass size spectra during the wet season, including primary biological aerosols (PBA), marine aerosols, and long-range transported (LRT) African aerosols (Andreae *et al.* 2015, Martin *et al.* 2010, Moran-Zuloaga *et al.* 2018). Pollen, bacteria, spores, and fragments of biological material are examples of PBA emitted in the Amazon forest (China *et al.* 2016, Huffman *et al.* 2012, Pöhlker *et al.* 2012). LRT of aerosols from Africa is typically observed in the Amazon between December and April, consisting of Saharan dust and biomass burning aerosols from the Sahel region (Baars *et al.* 2011, Pöhlker *et al.* 2019, Saturno *et al.* 2018). LRT episodes are relatively frequent in the wet season (5 to 10 events per year), usually lasting from 3 to 10 days (Moran-Zuloaga *et al.* 2018, Rizzolo *et al.* 2017). During LRT episodes, concentration enhancements on aerosol mass, equivalent black carbon, crustal elements (Al, Si, Ti, Fe), and potassium are observed, providing key nutrients for Amazonian ecosystems (Martin *et al.* 2010, Moran-Zuloaga *et al.* 2018, Rizzolo *et al.* 2017, Saturno *et al.* 2018).

Aerosol particles constitute an essential ingredient for cloud formation and development, since they can act as cloud condensation nuclei (CCN), over which water vapor condenses, producing cloud droplets. Moreover, some particles, known as ice nuclei (IN), can initiate the formation of ice crystals inside clouds, providing faster growth to precipitable droplet sizes when compared to CCN, and thus influencing precipitation (Andreae and Rosenfeld 2008). Measurements and modelling indicate that biogenic SOA act as CCN in the Amazon forest, while IN consist of coarse mode PBA and LRT mineral dust particles from Africa. In addition, coarse mode aerosols can act as giant CCN, generating large droplets and inducing rain in warm clouds (Pöhlker *et al.* 2016, 2018; Pöschl *et al.* 2010; Prenni *et al.* 2009). While aerosols provide nuclei for cloud formation, convective clouds may stimulate the formation of SOA particles through in-cloud processing of biogenic emissions (Figure 6.8), making an intrinsic connection between aerosol and cloud processes. An ensemble of observations demonstrates the biosphere-atmosphere integration in the Amazon, joining biogenic emissions, clouds, and precipitation, depicting the forest as a biogeochemical reactor. The biosphere emits BVOCs and aerosols, which are processed by photochemistry, providing nuclei for the formation of warm and cold clouds, which result in precipitation, sustaining the hydrological cycle and biological reproduction, closing a virtuous cycle (Pöhlker *et al.* 2012, Pöschl *et al.* 2010).

6.5.3 Ozone and Photochemistry

Ozone (O_3) is a highly reactive trace gas, with largely varying atmospheric concentrations globally. There is no significant direct source of tropospheric O_3; therefore, its concentration strongly depends on precursors like NO_X, CO, and VOCs (Rummel *et al.* 2007, Yáñez-Serrano *et al.* 2015, Lu *et al.* 2019) and to a smaller extent on the exchange between the stratosphere and troposphere (Ancellet *et al.* 1994, Hu *et al.* 2010). Lifetime of O_3 depends on atmospheric chemistry, which is controlled by temperature and radiation. The globally-averaged lifetime of tropospheric O_3 is approximately 23 days (Young *et al.* 2013), but due to surface deposition and chemical reactions it is much shorter in the boundary layer (Cooper *et al.* 2014), which can lead to strong gradients between a well-mixed boundary layer far from strong precursor emission sources and the free troposphere. Concentrations above the oceans or at remote, undisturbed continental areas are significantly lower than those of the surroundings of cities and burning biomass. Hence, the remote Amazon rainforest has turned out to be an ideal place to study O_3 chemistry under nearly pristine conditions. This property has drastically changed due to increased biomass burning and deforestation, which leads to strongly enhanced NO_X and O_3 concentrations over most parts of the Amazon Basin, especially during the drier season between July and October. The strongest sink of O_3 is dry deposition, which can occur through stomatal and nonstomatal uptake by leaves. Soil and water surfaces can additionally act as O_3 sinks (Clifton *et al.* 2020). Analyses of turbulence transport of tropospheric air into the forest combined with O_3 flux measurements can improve the evaluation of these processes. Mixing ratios of O_3 above 40 ppb, which also occur in the remote Amazon due to biomass burning, are known to cause damage to leaves (Pacifico *et al.* 2015) due to generation of reactive oxygen species that can induce cell death and lesions (Clifton *et al.* 2020). Hence, even remote areas far away from biomass burning can be very negatively affected by air pollution transported over several hundreds of kilometers.

6.6 Conclusions

The Amazon is a key feature of the planetary biosphere; its biogeochemical cycles are major factors for the environment and climate, and form the largest single-biome contribution to many key planetary biogeochemical processes. Geological and climatic variability across the Amazon plays an important role in shaping the features of the region's biogeochemistry and ecosystem functions. The exchange of trace gases, such as greenhouse gases and reactive gases, and secondary and primary particles, contribute directly and/or indirectly to the greenhouse effect and affect atmospheric chemistry and physics. Emission (production) and deposition (uptake) processes affect the current concentration of greenhouse gases such as methane, carbon dioxide, ozone, and nitrous oxide. Reactive trace gases affect the oxidative capacity of the atmosphere with significant influences on particle production and cloud condensation processes. Hence, climate is affected at local, regional, and global scales, including atmospheric warming, chemical processing in the atmosphere, and hydrology. Continued degradation of the Amazonian rainforest and passing of tipping points would result in a weakening and potential collapse of the biogeochemical network reaching from the soil and forest up to the atmosphere. This would have severe consequences for Amazonian ecosystems and for the communities that rely on them.

6.7 Recommendations

- There is a need to better understand and create an early warning system for the stability of the Amazon carbon store and sink in light of global environment change. Loss or reversal of the Amazon carbon sink would have global consequences and make it more difficult to limit peak warming to the internationally-agreed target of 1.5°C or 2°C.
- There is a need to better quantify and map the sources and sinks of methane and N_2O in the Amazon system.
- The potential role of the Amazon biome and its associated atmospheric chemistry in influencing cloud properties and regional and global climate needs to be better quantified and may be amongst the most significant contributions of the Amazon to planetary function.

6.8 References

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Amazon Assessment Report 2021

Cross Chapter 1

The Amazon Carbon Budget

Rio Parima na Terra Indígena Yanomami (Foto: Bruno Kelly/Amazônia Real)

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Cross-Chapter: The Amazon Carbon Budget

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Abstract

The main objective of this cross-chapter is to summarize the status of the Amazon as a source or sink of carbon (C). The processes and studies involved are detailed in other SPA chapters. The major challenge of determining the Amazon's status as a net C source or sink at a continental scale is that many complex processes contribute to C fluxes. Unlike in other regions, emissions from the burning of fossil fuels are minor contributors to Amazonian fluxes. Instead, the major sinks and sources of C to the atmosphere are associated with the net accumulation or loss of biomass, with losses including deforestation, biomass burning, and tree mortality followed by decomposition. Biomass accumulates in areas where tree growth exceeds losses. The Amazon includes not only intact forests, also but degraded and logged forests, natural non-forests, agricultural and urban areas, and aquatic systems including wetlands that all contribute to regional carbon cycling.

Two methods are used to estimate land-atmosphere carbon balance at broad spatial scales. Bottom-up estimates use field measurements of biomass accumulation and loss (through mortality) in plots, and scale these based on remote sensing and modeling to characterize broad regions of similar vegetation type. Top-down approaches use measurements of CO_2 concentrations taken by satellites and aircraft together with atmospheric transport models to estimate net land-atmosphere fluxes. These fluxes represent all processes, including deforestation, degradation, forest mortality, imbalances between respiration and photosynthesis during dry season stress, biomass burning, agricultural activities, fossil fuel emissions, regrowth of secondary forests, and growth of intact (primary) forests. While forest plot measurements have been in place for several decades, only in the last decade or so have measurements of biomass change from satellites, aircraft, or airborne sensors been available. Thus, estimates of the net C balance at the scale of the whole Amazon have only been produced for the last decade, and there are high levels of uncertainty associated with the integration of different approaches, process, and regions.

Results from top-down and bottom-up studies for the period 2010 through 2019 indicate that the Amazon region as a whole, including all uptake and loss processes describe above, is a carbon source on the order of 0.30 ± 0.20 Pg C y^{-1} and 0.23 ± 0.20 Pg C y^{-1}, respectively. It is important to acknowledge and understand the assumptions behind these two approaches, and further research is needed to understand and reduce differences between them.

CB1. CO_2 Uptake and Emissions

During the last 40 to 50 years, the Amazon has experienced strong human impacts from deforestation and land use change. According to the Brazilian Annual Land Use and Land Cover Mapping Project (Mapbiomas Amazonia 2020), a cumulative total of 17% was deforested by 2019, of which

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agriculture represents 14% (89% pasture and 11% crops) (MapBiomas Amazonia 2020). Inventories from long-term forest plot networks (e.g., RAINFOR), many beginning in the 1980s, provide data on carbon dynamics for intact, mature forests at nearly 300 sites. These individual plots, scaled to the total forested area, indicate that intact forests are a net sink for carbon, although the rate of carbon uptake has decreased over the past three decades, mainly due to increases in mortality (Brienen *et al.* 2015; Phillips and Brienen, 2017; Hubau *et al.* 2020) (see Chapter 6). The carbon sink or uptake (i.e., carbon removal from the atmosphere, reported here with a negative sign) estimated for mature upland forests, scaled to an area of 7.25 x 10^6 km^2, results in an estimate of mean net carbon uptake in intact forests for the 1990s of -0.59 ± 0.18 Pg C y^{-1}. In the first decade of the 2000s, carbon uptake decreased to -0.41 ± 0.20 Pg C y^{-1}, and in the decade of the 2010s was -0.22 ± 0.30 Pg C y^{-1} (see Table CC1; note all studies were scaled to the same area). Reported uncertainties are those reported in the publications and based on the variability among studies. According to these studies, the carbon sink has weakened by around 60% over the course of the last three decades; however, this decrease was not evenly distributed across the Amazon basin (Phillips and Brienen 2017). Historical deforestation and degradation affect the dry season, producing a dryer, hotter, and longer dry season; this is associated with climate trends that make forests more susceptible to fire and increased tree mortality, affecting carbon sinks, including in adjacent forests not directly impacted by fire. These fluxes also vary geographically (Gatti *et al.* 2021).

In the last decade, complementary bottom-up studies have focused on estimating carbon emissions and uptake from different land use and land cover changes (LUCC) (Aguiar *et al.* 2016; Assis *et al.* 2020; Aragão *et al.* 2018; Silva Junior *et al.* 2020; Crippa *et al.* 2019; Smith *et al.* 2020). These studies combined knowledge derived from fieldwork and remote sensing in models. The INPE-EM model (Aguiar *et al.* 2016; Assis *et al.* 2020) considered all LUCC components, and the results are similar to those of component-specific studies (Assis *et al.* 2020; Baccini *et al.* 2017), indicating positive net emissions related to LUCC processes of around 0.37 to 0.48 Pg C y^{-1}. However, there are many uncertainties in such measures, related to estimating actual C emissions during biomass burning, processes of loss, and uptake subsequent to disturbance. All studies in Table CC1 and CC2 are scaled to the area of the Amazon *sensu latissimo*, i.e., the entire Amazon Rainforest ecoregion without the Planalto (cerrado) (as delineated in Figure CC.2b) (Eva et al. 2005). Studies done in the Brazilian Amazon were scaled to the Amazon *sensu latissimo* without the Brazilian Planalto, based on the proportion of deforested area based on MapBioma analyses for both regions.

Based on eddy flux towers (Restrepo-Coupe *et al.* 2013; Saleska *et al.* 2013) and aircraft vertical profiles (Gatti *et al.* 2021), Figure CC.1 illustrates regional differences in carbon flux related to land use change and the occurrence of intact forests. In general, more carbon is absorbed in the western Amazon than the eastern (Malhi *et al.* 2015; Gatti *et al.* 2021) (see Chapters 4 and 6). Regional distributions of carbon emissions and uptake are shown in Figure CC.2 (adapted from Phillips and Brienen 2017), and are associated with geographical differences in climate (mainly the dry season), deforestation, and carbon sinks or sources (Gatti *et al.* 2021).

As noted in Chapter 6, rivers and associated floodplains move and distribute carbon laterally across the Amazon. High rates of gross and net primary production (GPP and NPP) by plants occur in Amazonian aquatic environments, and large amounts of carbon dioxide are emitted from rivers, lakes, and wetlands (Richey *et al.* 2002; Melack *et al.* 2009). Photosynthetic activity by emergent trees and herbaceous plants fixes atmospheric CO_2 and adds organic carbon or respired CO_2 to aquatic environments. Algal (phytoplankton and periphyton) NPP derived from dissolved inorganic carbon is smaller, mostly recycling carbon within the aquatic environment. Few measurements of flooded forest productivity are available, and photosynthesis by herbaceous plants is difficult to extrapolate spatially from specific sites. Hence, the estimates of water to atmosphere fluxes of 0.7 Pg C y^{-1} in Table CC1 have considerable uncertainty and large seasonal and interannual variability (Melack *et al.* 2009; Abril *et al.* 2014) (see Chapter 6). Annual inputs of carbon are estimated to be of similar order to estimates of CO_2 degassed from these habitats.

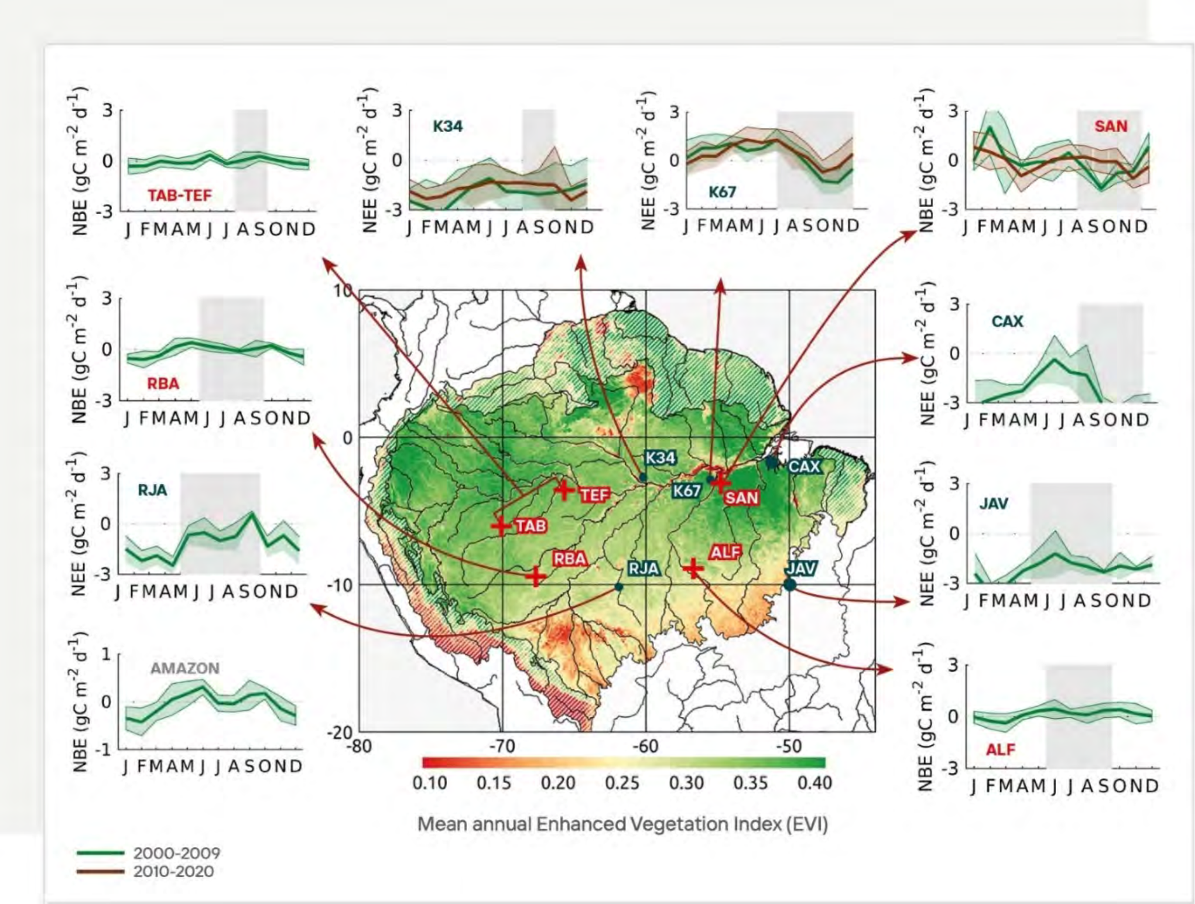

Figure CC.1 Map of mean annual Enhanced Vegetation Index (EVI) across the Amazon (scale at bottom, with greener colors indicating more photosynthesis; BRDF corrected MCD43C1 product for solar zenith angle of 15º and observed in nadir view (Schaaf and Wang 2015). Location of eddy covariance forest tower sites (Restrepo-Coupe *et al.* 2013, Saleska *et al.* 2013) (black dots) where measurements of annual average cycles of net ecosystem exchange (NEE) were included in this analysis (graphs in margin, gray shading indicates dry season months): Manaus forest (K34) 1999–2006, Santarém forest (K67) 2001–2005, 2008-2011 and 2015-2019, forest of Caxiuana (CAX) 1999-2003, Reserva Jarú southern forest (RJA) 2000-2002 and the seasonal inundated forest of Bananal (JAV) 2003-2006. Location of vertical profile sites (red crosses), and monthly mean net biome exchange (NBE) from the aircraft vertical profiles (2010-2018) at Santarem (SAN), Alta Floresta (ALF), Rio Branco, Acre (RBA), and Tabatinga (TAB; measures taken from 2010 to 2012) and Tefé (TEF; measures taken from 2013). Amazonian monthly mean NBE (2010-2018) was based on the weighted mean of fluxes for the 4 aircraft vertical profile sites (Gatti *et al.* 2021). The regions of influence for each vertical profile site are presented at Figure CC2b.

Hence, inputs and emissions of CO_2 in aquatic environments are approximately in balance, when integrated over the whole basin.

For the last decade (2010 through 2019), top-down studies based on vertical profiles, satellite data, and modelling provide estimates of the Amazon's carbon balance. These studies show large interannual variations. Top-down estimates indicate the Amazon as a whole is a carbon source (losses to the atmosphere) on the order of +0.30 ± 0.20 Pg C y^{-1} (Gatti *et al.* 2014; Feng *et al.* 2017; Baccini *et al.* 2017; Assis *et al.* 2020; Gatti *et al.* 2021), where mean fire emiss ions represent 0.44 ± 0.10 Pg C y^{-1} (Gatti *et al.* 2014, 2021; van der Laan-Luijkx *et al.* 2015; Baccini *et al.* 2017) (Table CC1) and mean forest uptake is -0.15 ± 0.20 Pg C y^{-1} (van der Laan-Luijkx *et al.* 2015; Alden *et al.* 2016; Baccini *et al.* 2017). These studies include all processes in the Amazon, including sinks in mature and secondary forests, recovery from disturbed forests, and carbon emissions from deforestation, degradation, logging, decomposi-

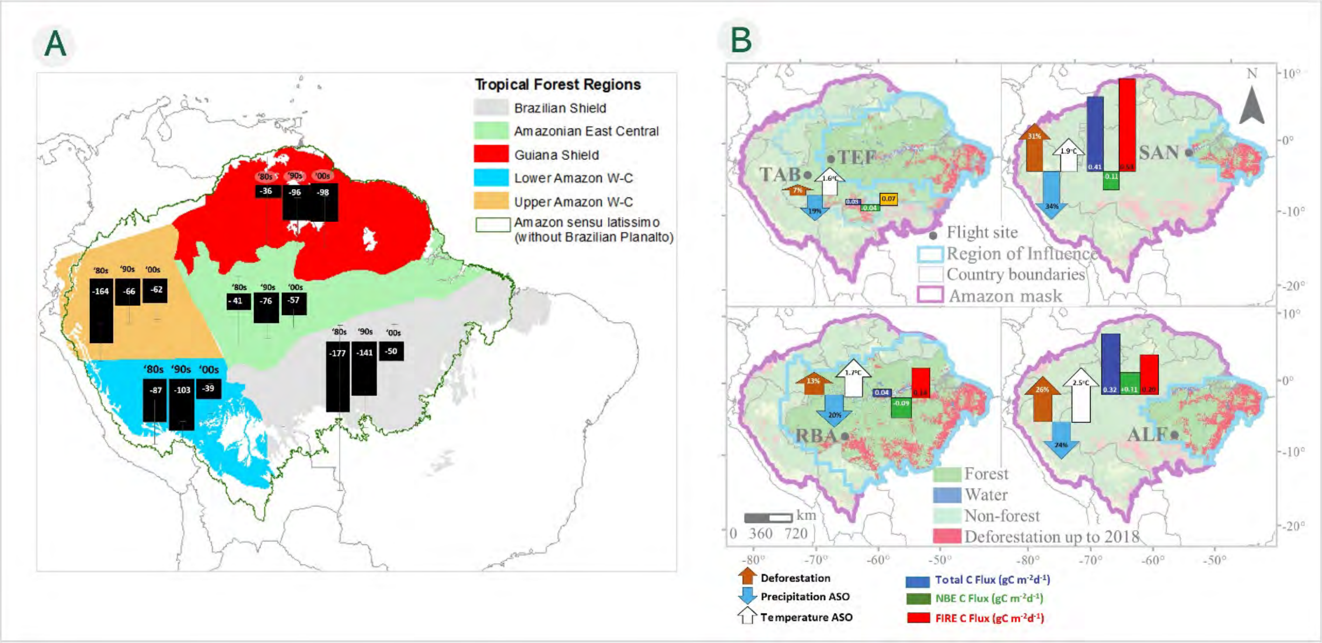

Figure CC.2 A) Amazon carbon fluxes in mature forests 1980s–2000s per region (black bars), measured in long-term plots of the RAINFOR network. Negative values represent uptake. Units are in Tg carbon per year (10^{12}g C y^{-1}). Adapted from Phillips and Brienen (2017) and Feldpausch *et al.* (2011). B) Accumulated deforestation per region of influence (limited by light blue lines) for vertical profiles sites (orange arrows), 40-year reduction in precipitation during the months of August, September and October (ASO) (light blue arrows), increase in temperature in ASO (white arrows) and 2010-18 carbon fluxes (Total: dark blue bars, net biome exchange (NBE): green bars, fire: red bars) (Gatti *et al.* 2021).

tion, fires, fossil fuels, and agriculture (pasture and crops).

For the last decade (2010 through 2019), bottom-up studies indicate that mature forests are carbon sinks of -0.22 ± 0.30 Pg C y^{-1} (Brienen *et al.* 2015; Phillips and Brienen, 2017; Hubau *et al.* 2020), and secondary forests -0.10 ± 0.02 Pg C y^{-1}. Carbon emissions include forest fires of 0.20 ± 0.20 Pg C y^{-1} (van der Werf *et al.* 2010; van der Laan-Luijkx *et al.* 2015; Baccini *et al.* 2017; Aragão *et al.* 2018; Silva *et al.* 2020), forest degradation, deforestation, and other carbon emissions of 0.32 ± 0.10 Pg C y^{-1} (Aguiar *et al.* 2016; Assis *et al.* 2020; Smith *et al.* 2020; Silva Junior *et al.* 2020), where fire emissions from deforestation are 0.05 ± 0.01 Pg C y^{-1} (Aguiar *et al.* 2016; Assis *et al.* 2020), representing 14% of total fires, included in the total fire emission estimate. Estimated energy sector emissions are 0.03 Pg C y^{-1} (Crippa *et al.* 2019). Combining mature forest growth, secondary regrowth, LUCC processes, and fire emissions (subtracting fires included in deforestation), the Amazon is currently a carbon source, representing 0.23 ± 0.20 Pg C y^{-1}, slightly less than the net emissions estimated from top-down studies. Large uncertainties, especially due to lack of knowledge about the emissions from degradation, decomposition, and fire emissions, (see Chapter 19) remain.

The results from top-down and bottom-up indicate that the Amazon as a whole is a carbon source, 0.30 ± 0.20 Pg C y^{-1} and 0.23 ± 0.20 Pg C y^{-1}, respectively.

Table CC.1 Amazon carbon balance, from bottom-up and top-down studies of various sources (C losses) and sinks (C uptake) for the area of 7.25 x 10^6 km^2.

	Period	C uptake (PgC y^{-1})	C losses (PgC y^{-1})	Total C Balance (PgC y^{-1})
Bottom-up studies				
Phillips and Brienen 2017 (Mature forest growth: uptake; LUCC: losses)	1990-99	- 0.54 ± 0.18	0.27 (LUCC)[1]	-0.27
	2000-09	- 0.38 ± 0.20	0.28 (LUCC)[1]	-0.10
	2010-19	- 0.20[2]		
Brienen *et al.* 2015 (Mature forest growth: uptake; LUCC: losses)	1990-99	- 0.62 ± 0.09		
	2000-09	- 0.44 ± 0.10		
	2010-19	- 0.23[2]		
Hubau *et al* 2020 (Mature forest growth: uptake; LUCC: losses)	1990-99	-0.68 ± 0.15		
	2000-09	-0.45 ± 0.13		
	2010-19	-0.25 ± 0.30		
INPE-EM System[3,4] (Deg+Def+SF, not PF)	2010-19	-0.16 ± 0.01	0.34 ± 0.09	0.18 ± 0.09
Assis *et al.* 2020[3] (Deg+Def+SF, not PF)	2007-16	-0.15 ± 0.02	0.37 ±0.08	0.23 ± 0.13
Aguiar et al. 2016[3] (Deg+Def, not PF/SF)	2007-13	-0.06 ±0.003	0.26 ±0.06	0.20 ± 0.11
Silva Jr. *et al.* 2020 (Deg+Def)	2001-15		0.26 ± 0.05	
Smith et al, 2020[3] (Secondary forests)	1985-17	- 0.10 ± 0.02		
GFED (Global fire data)	2010-18		0.18	
Aragao *et al.* 2018 (Fire emissions)	2003-15		0.21 ± 0.23	
Crippa *et al.* 2019 (EDGAR data base)[5]	2015		0.03	
Bottom-up Total balance 2010-2020		**- 0.32 ± 0.20[6]**	**0.55 ± 0.20[7]**	**+ 0.23 ± 0.20**
Aquatic systems				
Rivers			0.14 ± 0.04	
Lakes and floating plants			0.03 ± 0.01	
Streams			0.10 ± 0.03	
Forested floodplains			0.26 ± 0.8	
Other wetlands			0.16 ± 0.5	
Hydroelectric reservoirs			0.01 ± 0.003	
Total aquatic C balance		**-0.7 ± 0.3**	**0.7 ± 0.2**	**~0**
Top-down Studies				
Gatti *et al.* 2021 (Aircraft/ Inv. modeling)	2010-18	- 0.12 ± 0.40 (NBE)[8]	0.41 ± 0.05 (Fire)	0.29 ± 0.40
Gatti *et al.* 2014 (Aircraft/ Inv. modeling)	2010-11	- 0.15 ± 0.18 (NBE)[8]	0.43 ± 0.10 (Fire)	0.28 ± 0.14
Alden e*t al.* 2016 (Regional Bayesian Inversion modelling)	2010-12	-0.14 ± 0.32		
Van der Laan-Luijkx *et al.* 2015 (models: IASI, GFED4, GFAS, FINN, SiBCASA-GFED4)	2010-11	-0.27 ± 0.42[9]	0.24 ± 0.42 (Fire)[9]	
Feng *et al.* 2017 (Satelite/aircraft/modeling)	2010-14			0.32 ± 0.14
Baccini *et al.* 2017(MODIS pantropical satellite and modeling)	2003-14	-0.18 ± 0.02	0.48 ± 0.07	0.30 ± 0.07
Top-down Total balance 2010-20		**- 0.15 ± 0.20**	**0.44 ± 0.10**	**+ 0.30 ± 0.20**

1- LUCC land-use changes—including fragmentation and edge effects, logging, fire, secondary re-growth and subsequent disturbance
2- Extrapolated using the trend
3- Scaled to Amazon *sensu latissimo*, without Planalto using MapBiomas deforestation
4- INPE-EM Operational System: http://inpe-em.ccst.inpe.br/en/
5- Energy sector, Industrial Processes and Product Use, and Agricultural waste burning
6- Uptake PF + SF (-0.22 + (-10)). Primary Forest (PF), Secondary Forest (SF);
7- Losses Assis (2020) losses from Deforestation (Def) + Degradation (Deg): 0.37 + Fire: 0.15 (0.20 - 0.05 (computed by Assis)) + energy: 0.03
8- NBE (Net Biome Exchange: Total C flux less Fire);
9- Qualitative results for comparison between 2010 and 2011, not used quantitatively.

Table CC.2 Methane Emissions

	Period	**CH_4 uptake**	**CH_4 Fire emission**	**Total CH_4 emission**
Area normalized 7.25 x 10^6 km^2		**($TgCH_4$ y^{-1})**	**($TgCH_4$ y^{-1})**	**($TgCH_4$ y^{-1})**
Bottom-up studies				
Natural emissions				
Rivers				0.7 ± 0.2
Lakes				0.7 ± 0.2
Streams				0.4 ± 0.2
Forested floodplains				
Flux from water surface				16.4 ± 5
Flux from trees				18.2 ± 5.5
Flux from exposed soil				1.1 ± 0.2
Other wetlands				7 ± 2
Upland soils*		1.0 - 3.0		
Anthropogenic				
Hydroelectric reservoirs				2.0 ± 0.6
Energy sector**	2015			0.8
Waste**	2015			0.5
Agriculture**	2015			4.7
Top-down Studies				
Aircraft/Modelling Studies				
Basso *et al.* 2021	2010-18		7.7 ± 1.6	46.2 ± 10.3
Wilson *et al.* 2021	2010-13			40.1 ± 5.6
	2014-17			47.9 ± 5.5
Pangala *et al.* 2017 (Column Budget Technique)	2010-13		4.2 ± 0.7	46.2 ± 6.1
Wilson *et al.* 2016 (3-D atmospheric chemical transport model)	2010-11		2.2 ± 1.5	37.5 - 50.8
Satelite/modelling Studies				
Bergamaschi *et al.* 2009 (inverse modeling + revised SCIAMACHY retrievals)	2004			40.0 – 44.7
Fraser *et al.* 2014 (inverse modeling and GOSAT)	2010			44.6 ± 2.4

* Estimated by Davidson and Artaxo 2004

** Emissions based on EDGAR database for the year 2015

CB2. Methane Emissions

Descriptions of terrestrial and aquatic methane fluxes, processes, and the CH_4 budget are provided in Chapter 6. For comparison to the CO_2 budget, we scaled CH_4 estimates to the same area (7.25x10^6 km^2); a proportional adjustment based on the two areas and assuming sufficiently similar habitats are represented. Top-down and bottom-up estimates for this region have reasonable agreement given the considerable uncertainties in these fluxes (Table CC2). Fluxes of CH_4 from natural aquatic environments in the Amazon Basin are estimated to be approximately 44.5 Tg CH_4 y^{-1}. Interannual variations in the area of inundated habitats and highly variable fluxes associated with ebullition outgassing by trees, and temporal and spatial differences in dissolved CH_4 concentrations and gas exchange velocities (Melack *et al.* 2004; Pangala *et al.* 2017; Barbosa *et al.* 2020) make uncertainty estimates only approximate. Estimates of anthropogenic CH_4 emissions based on the EDGAR v.5.0 model include energy production, agriculture, industrial processes, product uses, and waste management. These sources contribute 6 Tg CH_4 y^{-1}, with emissions from agriculture responsible for 78% and enteric fermentation the main source from this sector (93%), highlighting the importance of cattle in anthropogenic Amazonian methane emissions. Fluxes from the 159 medium to large hydroelectric reservoirs currently in the Amazon Basin, excluding those in the lower Tocantins Basin and including major ones in Venezuela, Suriname, and French Guiana, total 2 Tg CH_4 y^{-1}.

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Chapter 7

Biogeophysical Cycles: Water Recycling, Climate Regulation

Rio Parima na Terra Indígena Yanomami (Foto: Bruno Kelly/Amazônia Real)

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Graphical Abstract

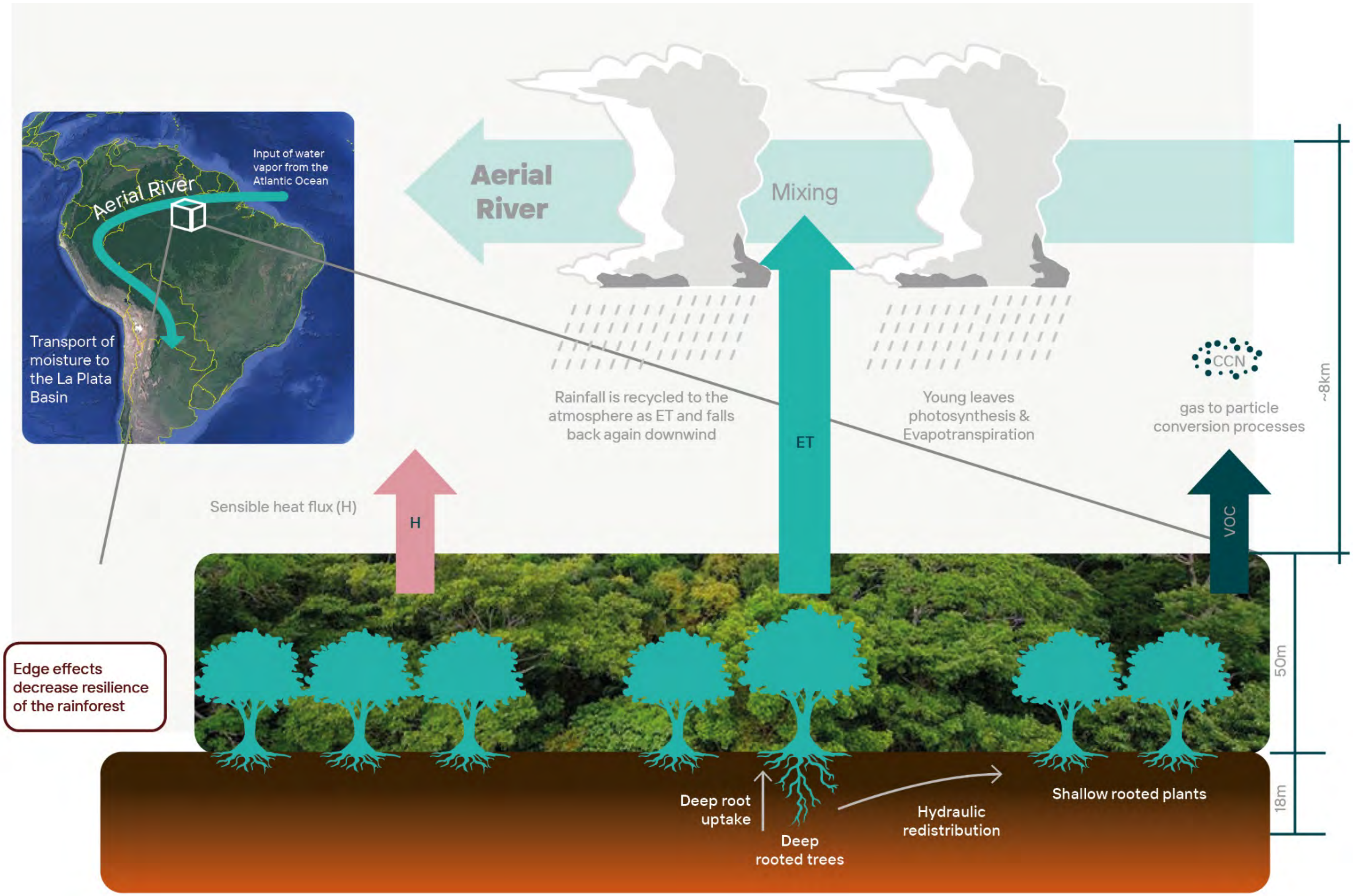

Figure 7.A Graphical Abstract

Biogeophysical Cycles: Water Recycling, Climate Regulation

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Key Messages

- The Amazon rainforest can cycle large amounts of water vapor from the soil to the atmosphere via evapotranspiration (ET). The Amazon basin's average recycling ratio varies from 24% to 35%, with a median value of 28%.
- The central and northwestern parts of the Amazon export moisture to the Andes via diverse atmospheric (or aerial) rivers that supply water for tropical glaciers, páramos, and cities. The south-western part of the Amazon Basin is an important direct source of moisture for the La Plata Basin year-round, with moisture transported via the South American low-level jet.
- The amount of forest cover regulates the local temperature and the amount and timing of precipitation, with forest loss (increase) leading to reductions (increases) in rainfall and subsequent impacts on forest cover. Locally, the replacement of deep-rooted rainforest trees with grasses or crops warms the microclimate because of lower ET, despite higher albedo of senesced vegetation. If affected areas are large enough, this can affect rainfall, especially at the end of the dry season, with implications for forest degradation, forest flammability, and crop yields.
- The most important changes in the hydroclimate system occur in the transition between the dry and rainy seasons, with a lengthening of the dry season in regions affected by meso- to large-scale (10-1,000 km^2) deforestation, which has important ecological and hydrological consequences. Future studies should focus on these seasonal transitions.
- Very few (if any) of the new advancements in forest edge degradation have been included in the processes simulated by Earth System Models (ESMs). Projecting the future of Amazonian forests requires a better representation of forest edge effects in ESMs.

Abstract

The warm and humid climates that sustain Amazonian rainforests are partly a consequence of interactions between the forest and the atmosphere. This chapter assesses the biogeophysical processes by which the rainforest provides moisture and energy to maintain its own climate. A combination of several plant traits and processes – low albedo, rough canopies, deep rooting, plant hydraulic lift, and biological regulation of water flux through leaves – allows the capture of water stored at deep soil layers. These mechanisms provide a steady flow of water vapor into the atmosphere, which is recycled internally in the Amazon and is a major water vapor source to other South American regions. Regionally averaged, about 28% of the rainfall in the Amazon has fallen at least once, with this fraction increasing westward, until it exceeds 50% at the foot of the Andes. The rainforest also plays an important climate regulation role in the southern Amazon during the dry-to-wet season transition (Sep-Oct). Forested areas have an early onset and late end of the rainy season (Oct-Apr). They are also associated with a low frequency of dry spells of

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any duration in the transition months between the dry and the rainy seasons (Mar-Apr, Sep-Oct) when compared to highly deforested areas. Finally, the intense loss of latent heat through ET maintains air temperature below 30°C, which is near-optimal for photosynthesis, and consequently, carbon uptake.

Keywords: Aerial rivers, deep soil moisture capture, temperature regulation

7.1 Introduction

The Amazon is well known for two remarkable characteristics: the rainforest and its warm and humid climate. The Amazon rainforest is perhaps the most luxuriant biome globally, with high biomass, tall canopy, and rich biodiversity (Chapter 3). The annual long-term average of rainfall ranges from 2,000 to 2,300 mm, depending on the period used for calculation and whether the Tocantins Basin is included or not (Table 1, Chapter 5). In the rainiest parts of the region, rainfall may reach 6,000-7,000 mm/yr at the Andes' feet (Section 5.3.5, Chapter 5). A “relatively dry season” is found in specific places, such as the southern border of the Amazon, near the transition to the cerrado (savannas of Central Brazil), and in the south-north axis around Santarém (in Pará State, Brazil). “Relatively dry season” describes a season in which the monthly mean precipitation is below monthly ET rates, but still presents high precipitation amounts (~100 mm/mo, as defined by Sombroek 2001). A six-month-long dry season is found on the upstream areas of the southern tributaries of the Amazon River (Tapajós and Xingu rivers), in most of the Tocantins Basin, in the state of Roraima (Brazil), and to the north of Boa Vista (Roraima’s capital city), where annual rainfall can be as low as 1,500 mm. Monthly mean temperatures vary between 26°C and 28°C for the lowland Central Amazon, and the annual mean decreases with altitude. In the Andean highlands, the annual mean temperature is 12.6°C in Sucre, Bolivia (elevation 2,800 m), 12.8°C in Cajamarca, Peru (2,740 m), and 6.8°C in La Paz, Bolivia (3,650 m). Seasonality (monthly mean temperature amplitude) increases with latitude, varying from about 2°C near the equator to about 4°C in Brasília (16°S). For locations of the cities, rivers, basin, and biome borders, refer to Figure 7.1.

These two remarkable characteristics – the luxuriant forest and the warm and humid climate – are intrinsically connected by two-way biogeophysical interactions, or cycles. Obviously, the presence of the rainforest in the Amazon is a consequence of the rainy climate that exists there; the tropical rainforest could not grow in a cool or dry environment. However, the functioning of the rainforest also helps produce the warm and humid climate necessary for its permanence. The rainforest interacts with the atmosphere in several ways, which affects the local, continental, and global climate. A major process is the recycling of water (Section 7.2.1). Following the water cycle process, winds near the ocean surface bring moisture from the tropical Atlantic Ocean into the Amazon. Part of this moisture falls as rain, and a portion of the fallen rain may quickly be returned to the atmosphere by the forest through evapotranspiration (ET). Some of this water vapor will come back as rainfall over the rainforest, and some is transported to neighboring regions.

This injection of water vapor does not present significant seasonal or interannual variability, which may be explained by several traits and processes associated with the rainforest, such as deep root capture, hydraulic redistribution, and biological synchronization of new leaf emergence with the dry season (Section 7.2.2).

This chapter assesses the biogeophysical interactions between the Amazon rainforest and the climate. A historical perspective is presented, highlighting breakthroughs that improved our understanding of the mechanisms by which the rainforest interacts with the atmosphere.

Figure 7.1 Orientation map. Biome map of South America, with main rivers and towns. Sources: WWF (https://www.world (wildlife.org/publications/terrestrial-ecoregions-of-the-world), RAISG (2020), WCS- Venticinque (2016).

7.2 The role of forests in water recycling

7.2.1 Water recycling in the Amazon

7.2.1.1 General concepts about water recycling

Water recycling is the process by which ET in a specific location on the continent contributes to precipitation in another place on the continent (Zemp *et al.* 2014). The recycling ratio (ρ) is the ratio of precipitation of continental origin divided by the total precipitation. It depends on several conditions, including spatial scale, the ratio of local ET to other water vapor sources, and the extension of the region downwind.

First, consider the scale. At one extreme, on the global scale, all water molecules evaporate from the Earth's surface, stay in the atmosphere for a few days, and then precipitate back. The recycling ratio is then 100%. At the other scale extreme, an infinitesimal area on the land surface, the probability that a water molecule that evaporates from that area precipitates back inside it is near zero (Eltahir and Bras 1996). A large region like the Amazon tends to have a high recycling ratio, but in between these two scales, regional recycling is more complex.

Figure 7.2 explains the dependence of recycling on the extension of the region downwind. Consider two rectangular areas of the same size, but one has its main dimension across the dominant winds (Figure 7.2a), while the other has its main dimension alongside the prevailing winds (Figure 7.2b). All other conditions (moisture transport from the ocean, precipitation, and evapotranspiration rate) are the same. The longer the dimension of the region along with the dominant winds, the higher the recycling.

Moisture recycling can be calculated from any source region where it evaporates (i.e., the Amazon) to any destination region where it precipitates (e.g., the Amazon Basin itself, including the Andes or the La Plata Basin). This section will first explore the role of recycling within the Amazon Basin and then its role as a source of water to other regions.

7.2.1.2 Historical perspective on the studies of water recycling in the Amazon basin

Classical climatological texts (Sellers 1965; Budyko 1974) consider that local ET is of minor importance as a source of precipitable water over continents. However, this assumption may not be accurate over a continental area where the ET reaches high rates, such as tropical rain forests.

The classical methodology (see, for example, Budyko, 1974) to calculate the recycling of water via ET states that, for a stable climate and in the long term, if there is no recycling; the net advection of water vapor to a region would be balanced by the hydrological runoff. Thus, using atmospheric sounding and hydrological measurements, one can calculate the recycling.

Molion (1975) first suggested that precipitation over the Amazon depends highly on local ET. Using the classical methodology described above, he concluded that the advection of water vapor contributes only 44% of the Amazon Basin's rainfall, while local ET provides the remaining 56%. Continuing this work, Lettau *et al.* (1979) presented data on the variation of the ratio between the total precipitable water and the precipitable water of oceanic origin according to longitude. Since the main wind direction is from east to west, the increase in the proportion of precipitable water from sources other than the ocean suggests that this source is ET. They also calculated that 88% of the rainfall in the westernmost part of the Amazon is water vapor that has fallen at least once previously.

Dall'Olio *et al.* (1979) used concentrations of the stable isotopes ^{18}O and ^{2}H (deuterium) as tracers to study the origin of the precipitable water in the Amazon region. The different masses of isotopes in water cause a distillation that concentrates the heavier isotopes (^{18}O and ^{2}H) closer to the original source of the precipitation and increasingly light isotopes (^{16}O and ^{1}H) with every recycling stage along the way. They concluded that the water vapor

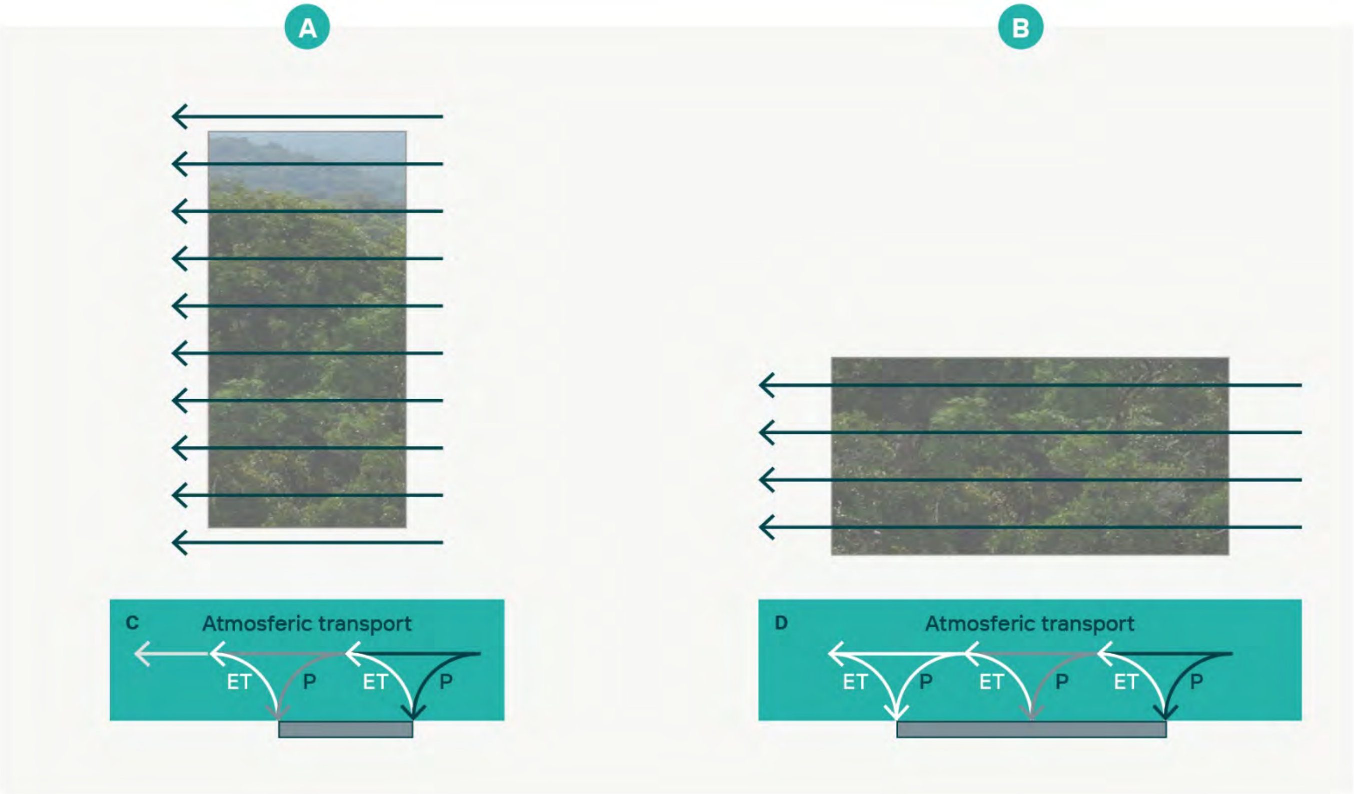


Figure 7.2 Schematic diagram of water recycling of two identical regions (A and B), differing only with respect to the wind direction. P is precipitation, and ET is evapotranspiration. Black arrows represent water vapor flux of oceanic origin, and white arrows indicate water vapor flux originated at the land surface. Shades of gray arrows represent the proportion of oceanic versus land surface water vapor.

flux from the ocean is smaller than the total precipitation over the basin, so it was necessary to consider at least one other water vapor source. Since there was no meteorological evidence of additional external sources of water vapor, they suggested that ET could provide the additional required moisture source. Their data indicated that, on average, both the sources (ocean and forest) are of the same magnitude, which suggests that the vegetation recycled 50% of the precipitation water.

Salati *et al.* (1979), using the same data of Dall'Olio *et al.* (1979), reported that, despite the Amazon basin's appearance as being a relatively uniform hydrometeorological unit, the seasonal and geographic variability of the isotopic data demonstrates the heterogeneity of the region from the hydrometeorological point of view, pointing out variations related to seasonality and location, with the Central and Western Amazon being areas where large amounts of water are recycled. In their classical review, Salati and Vose (1984) said that about 50% of the rainfall is from ET into the atmosphere, of which about 48% falls again as rain.

Nobre *et al.* (1991) calculated water budgets for the Amazon using atmospheric sounding data from the Global Tropospheric Experiment with at least two vertical profiles a day for a prolonged period. They concluded that about 50% of the rain originated from ET and 50% from moisture transport from outside the basin.

However, the soundness of these early estimates was limited by the low availability of the atmospheric sounding measurements, and several questions remained. First, climatological calculations of the recycled water ratio were not available. Second, the interannual variability of precipitation (ranging from 2,000 to 2,800 mm yr^{-1} in a 10-year return period) is much higher than the interannual variability of ET (see Section 5.4, and Chapter 5), and it was unclear how the sources of water vapor to precipitation vary simultaneously to the year-to-year variability of rainfall and ET.

In addition, these initial estimates considered that both the Andes and the Central Brazil plateau were important barriers to water vapor flux. Thus, they assumed that the water vapor flux out of the basin was close to zero. Moreover, Savenije (1996) demonstrated that, under this assumption, $\rho = 1 - C$, where C is the runoff coefficient, which is about 0.5 for the Amazon River. In conclusion, this assumption overestimated the recycling ratio. The ρ estimation did not improve until the next scientific breakthrough: four-dimensional global wind and moisture datasets.

7.2.1.3 Modern estimates

The advent of four-dimensional wind and moisture datasets in the 1990s (three space dimensions plus one time dimension), including atmospheric reanalysis products, allowed the calculation of spatial and temporal patterns of the recycling ratio. These datasets demonstrated that there is indeed a small flow of water vapor across the Andes, and a significant flow of moisture southward, towards central and southern South America (Section 7.2.3). Several studies used these datasets and different methods to calculate recycling, summarized in Table 7.1. The Amazon Basin's average recycling ratio varies from 24% to 35%, with a median value of 28%, or about half of what was previously estimated.

Of the estimates in Table 7.1, Staal *et al.* (2018) use a slightly different definition of water recycling. They count multiple evaporations of the same water molecule multiple times, yielding $\rho > 100\%$ in some months (see Staal *et al.* 2018, Fig. S5). This method also slightly overestimates the recycling ratio when compared to the other studies.

Even these more recent estimates may have limitations. Moisture tracking models vary widely in complexity, depending on the number of physical processes represented (Dominguez *et al.* 2020). Complex models are comprehensive in their physical representation, but computationally much more expensive. Simple models are faster to run, but focus on specific physical processes and simplify assumptions. A common assumption in simple models is that water vapor is well-mixed inside the atmosphere's vertical column. The well-mixing assumption can also be subdivided into several components, i.e., well-mixed during evaporation, transport, and precipitation. For example, the vertical height from where water vapor contributes to precipitation is not necessarily proportional to the level's specific humidity.

In regions where convective precipitation dominates, like the Amazon, water vapor from lower atmospheric levels contributes significantly more to precipitation than upper-level moisture, a process that has been called "fast recycling" (Lettau *et al.* 1979) and leads to an underestimation of terrestrial sources of moisture by simple models when compared to water vapor tracers in climate models (Goessling and Reick 2013; Dominguez *et al.* 2020).

On the other hand, there are models for tracing water vapor sources and pathways in the atmosphere that use Lagrangian particle tracking, like the NOAA HYSPLIT trajectory model (Stein *et al.* 2015) or the Weather Research and Forecasting regional climate model with Water Vapor Tracing (WRF-WVT) (Insua-Costa and Miguez-Macho 2018). These models explicitly simulate or parameterize processes like convection, microphysics, turbulence, and particle tracking, but have the disadvantage of being computationally expensive. Both methods (Eulerian and Lagrangian) can also be sub-divided into offline calculations (performed on previously generated datasets) or online calculations (performed while the model is running) (Dominguez *et al.* 2020). The online Lagrangian models, relying on prognostic water tracers built-into global or regional climate models, may provide

Table 7.1 Studies to calculate recycling.

Study	Method	Data Set	Period	ρ (%)
Brubaker *et al.* (1993)	Atmospheric bulk model	GFDL and NCAR	1963-1973	24
Eltahir and Bras (1994)	Atmospheric bulk model	ECMWF analysis	1985-1990	25
Trenberth (1999)	Atmospheric bulk model	CMAP and NCEP-NCAR reanalysis	1979-1995	35
Costa and Foley (1999)	Atmospheric bulk model	NCEP/NCAR reanalysis	1976-1996	30
Bosilovich and Chern (2006)	AGCM with passive water vapor tracers	initial conditions from the model; no time-evolving boundary conditions	1948-1997	27.2
Dirmeyer *et al.* (2009)	Quasi-isentropic back-trajectory (Lagrangian tracking)	NCEP/DOE reanalysis	1979-2003	28
van der Ent *et al.* (2010)	Eulerian atmospheric moisture tracking method	ERA-Interim reanalysis	1999-2008	28
Zemp *et al.* (2014)	Eulerian atmospheric moisture tracking method	TRMM for (P) and MODIS for ET	2001-2010	28
Zemp *et al.* (2014)	Eulerian atmospheric moisture tracking method	Land surface model for ET, average of CRU, GPCC, GPCP and CPC for P	1990-1995	24
Staal *et al.* (2018)	Eulerian atmospheric moisture tracking method/ cascade recycling	GLDAS	2003-2014	32

more physically consistent values. On the other hand, running them for a long time to calculate the climatological recycling ratio values will most likely lead to severe biases if boundary conditions are not constantly updated. In summary, all methods have advantages and disadvantages. It is unclear today what would be the effect of substituting the well-mixing assumption by the Lagrangian tracking on calculating the recycling ratio.

Nevertheless, these studies also concluded that the recycling ratio varies both spatially, seasonally, and interannually. Several authors, like van der Ent *et al.* (2010), Zemp *et al.* (2014), and Staal *et al.* (2018), provide spatially-explicit calculations of the recycling ratio. They show that ρ is close to zero near the mouth of the Amazon, where moisture from the ocean enters the Amazon, to >50% close to the Andes (Figure 7.3). The mechanical uplift from the mountains and the Andes' concave shape induce low-level convergence several hundred kilometers before the Andes, facilitating high precipitation rates and hindering moisture from crossing the Andes and leaving the basin.

Recycling is also higher during the dry season than during the wet season (contrast Figure 7.3a with Figure 7.3b). During the dry season, the input of moisture from the ocean decreases, and the steady flux of water from the rainforest increases the importance of this local source. As explained in Section 5.4 of Chapter 5 and below in Section 7.2.2, in most of the Amazon, ET is not controlled by the availability of soil moisture but rather by the availability of energy to evaporate water, hence the low seasonal variability. This is because Amazonian trees have access to water stored in deep soil layers and consequently do not suffer much water stress.

The stability of local ET is also associated with the variability of ρ at interannual and decadal time scales. For example, Costa and Foley (1999) found a weakening of the trade winds that transport water vapor from the tropical Atlantic ocean into the Amazon basin during 1976-1996, which caused a decrease in the input of water vapor to the Amazon Basin. In this case, the main source of water vapor to the basin decreased by about 720 mm/yr in 20 years (from 3,430 mm/yr in 1976-77 to 2,710 mm/yr in 1995-96, or 36 mm/yr^2); however, the Amazon Basin maintained precipitation and runoff by increasing the relative contribution of the local source of water vapor (regional ET) from 28% in 1976-77 to 33% in 1995-96.

7.2.2 Mechanisms to capture deep soil moisture by trees

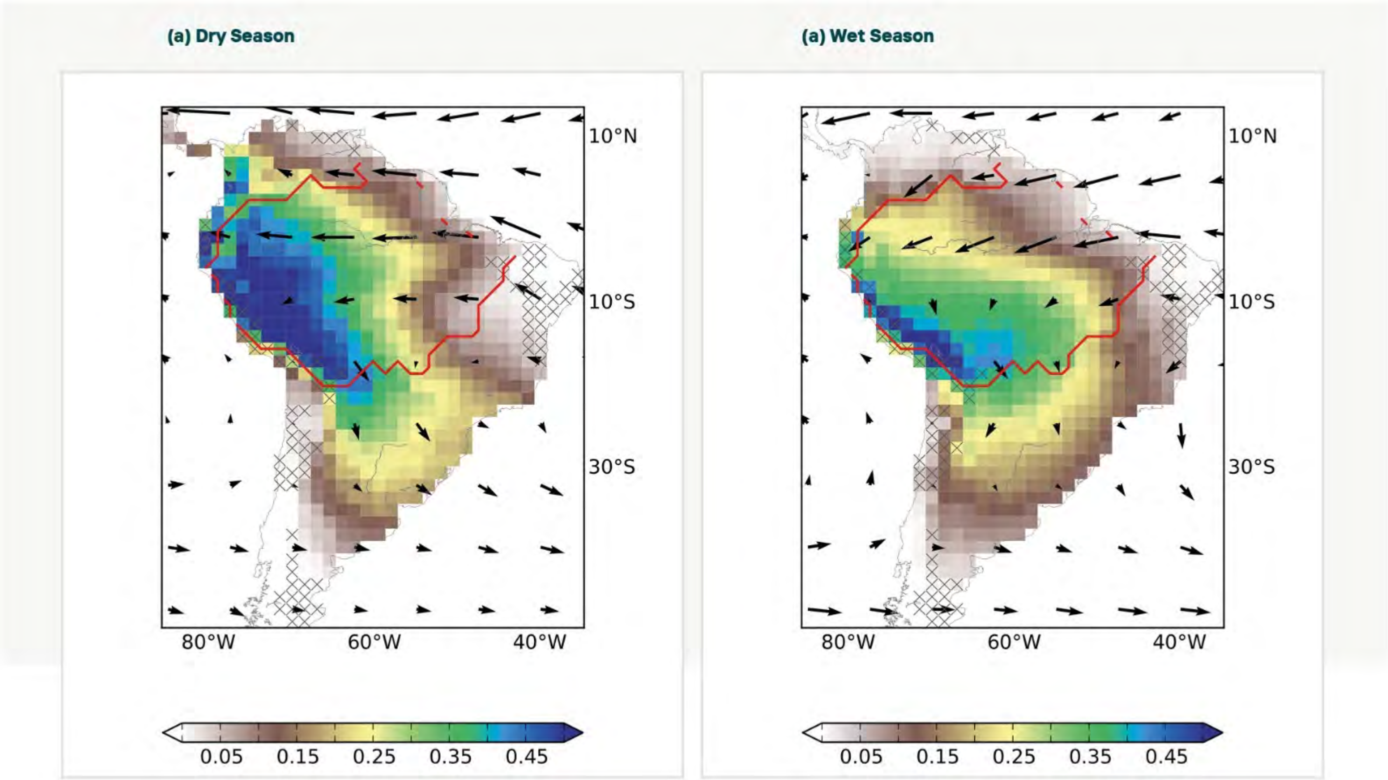


Figure 7.3 Fraction of precipitation originating inside the Amazon Basin (contour in red), using MOD16 ET data and TRMM precipitation data for the period 2001-2010, and direct moisture recycling calculations. (a) Dry season (Jun-Sep); (b) Wet season (Dec-Mar). Redrawn from Zemp *et al.* (2014).

Another breakthrough in understanding the rainforest's role in regional climate was direct measurement of ET using eddy-covariance techniques at several Amazonian upland forest experimental sites. These observations indicate that dry-season ET rates across central Amazonian forests peak during the dry season, consistently exceeding wet season values (Shuttleworth 1988). These observations imply that ET in these forests is regulated by the annual cycle of incoming radiation (which typically increases during the dry season due to a more vertical sun and diminished cloud cover), with dry season ET comparable to, or even consistently exceeding, wet season values (Hasler and Avissar 2007). The more complex seasonal ET dynamics of moisture-limited southern Amazonian upland forests indicates joint regulation by environmental (e.g., net radiation, vapor pressure deficit) and biological factors (forest canopy conductance) in these forests (Da-Rocha *et al.* 2009; Costa *et al.* 2010; Restrepo-Coupe *et al.* 2021).

These findings contradict common understanding (see the discussion between Werth and Avissar 2004, Costa *et al.* 2004), and simulation results from most land surface models, which show a decrease in ET and productivity during the dry season and drought periods because of water limitation (Christoffersen *et al.* 2014; see also Section 5.4 of Chapter 5).

This discussion focuses on upland forests' deep-water uptake mechanisms, as seasonally flooded forests are assumed to be less likely to be water-limited. Several studies have proposed different mechanisms to explain the drought (seasonal or extreme) tolerance of Amazonian rainforests. These mechanisms include deep-root water uptake, plant hydraulic lift, and leaf regeneration in the dry season.

As discussed in Chapter 5, Amazonian soils, due to their predominant clay texture in the plateau area, store, in the wet season, large amounts of rainfall that is released to plants during the dry season (Bruno *et al.* 2006; Chauvel *et al.* 1992; Hodnett *et al.* 1995; Nepstad *et al.* 1994). As the dry season progresses, this water tends to percolate and is stored in deep soil layers, which is mainly composed of the water infiltrated in the previous wet periods (Negron-Juarez *et al.* 2007), and where mainly deeper roots have the ability to take it up (Nepstad *et al.* 1994). Very deep (>6 m) fine roots, although rare, have been found in a few sites in the eastern (Nepstad *et al.* 1994) and central Amazon (Chauvel *et al.* 1992; Negrón-Juárez *et al.* 2020). In the eastern Amazon, where precipitation is more seasonal, Nepstad *et al.* (1994) found roots reaching 18 m. The existence of these roots, associated with low plant-available water in the upper (<1 m) soil layers, give rise to the understanding of the role of deep roots as the primary strategy of plants to deal with seasonal and, potentially, severe droughts (Bruno *et al.* 2006; Hodnett *et al.* 1995; Jipp *et al.* 1998; Nepstad *et al.* 1994).

Despite the documented occurrence of deep roots, it is well recognized that, in the Amazon, shallow roots (<1 m) are much more abundant than deep ones (Chauvel *et al.* 1992; Nepstad *et al.* 1994). The root density decreases from more than a kilogram of roots per cubic meter near the surface to a few tens of grams per cubic meter below two meters, being relatively constant below this level (Nepstad 1989, cited by Bruijnzeel 1996). Although deep roots have low density, research done by Hodnett *et al.* (1995) near Manaus has demonstrated that, in many years, it is impossible to close the dry season water balance of the Amazonian rain forest without using water stored at depths greater than 2 m. Markewitz *et al.* (2010), using data from a rainfall exclusion experiment in Santarém, also concluded that deep root water uptake contributions are crucial. Under control conditions, the 250 to 550 cm soil layer contributed ~20% of water demand, while the deepest layers (550–1,150 cm) contributed ~10%. Under the exclusion, root water uptake was sustained for the first 2 years of the experiment but declined after that.

Other studies have suggested the existence of mechanisms to transport water upward from deep to shallow soil layers, either through the root system, i.e., plant hydraulic lift (Dawson *et al.* 2002; Oliveira *et al.* 2005), or through fine-textured soils by the capillary rise mechanism (Fan and Miguez-Macho 2010; Romero-Saltos *et al.* 2005). However, hydraulic lift also relies on deep root water uptake and, when included in a land surface model, moderately increased the dry season ET rates (Lee *et al.* 2005). Capillary rise, in general, only drives water upward through a few centimeters (Romero-Saltos *et al.* 2005), and is more important in regions where the water table is shallow (Fan and Miguez-Macho 2010), which is not the case for most of the plateau areas where the water table is 30-40 m deep (Fan and Miguez-Macho 2010; Tomasella *et al.* 2008). Other studies have suggested the existence of a third mechanism, root niche partitioning (Brum *et al.* 2019; Ivanov *et al.* 2012), by which plants uptake soil water from different sources, as a function of their height, root depth, and plant hydraulic attributes such as resistance to xylem vessels embolism (Rowland *et al.* 2015).

Mechanisms of root access to soil water are also coupled to biological regulation of water flux through leaves. Because leaf stomata link ET to photosynthetic flux (Gross Primary Productivity, GPP), stomatal regulation that allows increasing dry season GPP (Huete *et al.* 2006; Wu *et al.* 2016; Saleska *et al.* 2016; see also Chapter 6) also facilitates the corresponding dry-season maxima in forest ET discussed above (Shuttleworth 1988; Hasler and Avissar 2007). Recent work shows that high dry-season leaf photosynthetic capacity and high stomatal conductance are both driven by leaf phenology, i.e., the biological synchronization of new leaf emergence and old leaf senescence during the dry season causes large shifts in canopy leaf composition toward younger, more conductive leaves, likely facilitating seasonal increases in ET in the central Amazon (Albert *et al.* 2018; Wu *et al.* 2016). Christoffersen *et al.* (2014) highlight the important complementary roles of root dynamics and leaf phenology in regulating ET.

In conclusion, if the rainforest is replaced with another land cover and use, the Amazon would not be able to keep ET at the same rate, particularly during the dry season. As a result, the rooting depths would be much smaller, hydraulic redistribution would cease, and the evaporating surface (leaf area) would be smaller and possibly present lower greenness than it does today.

7.2.2.1 The role of Amazon tropical forests producing its own climate

As said earlier, tropical rainforests are an obvious consequence of the warm and humid climate in that region. However, in the past decades, evidence is accumulating that the rainforest and the warm and humid climate are strongly connected, forming a two-way interacting system that perpetuates each other (positive feedback). In other words, the humid tropical climate allows the rainforest's existence, which, in turn, helps to produce the rainy climate it needs.

A rainy climate requires two necessary conditions: a humid atmosphere and sufficient ascending vertical motion to form clouds and induce precipitation.

As stated in previous sections, on an annual average basis in the Amazon, around 72% of the water vapor that enters the atmospheric column is of oceanic origin, and 28% is evaporated locally (Table 7.1). In addition to this role as a water vapor source, the evergreen tropical forest has yet another role in the local climate. Theoretical (Eltahir 1996; Zeng and Neelin 1999) and modeling studies (Dirmeyer and Shukla 1994) demonstrate that the rainforest's low albedo favors convection over the basin, while an increase in the surface albedo causes a subsidence anomaly over the region. In addition, forests also emit volatile organic compounds (VOCs, for example terpenes) that become cloud condensation nuclei (CCN) and favor the formation of rain droplets (see also Chapter 6). Because water vapor and convection are key contributors to precipitation, large-scale rainforests likely have some ability to maintain their own climate.

It is puzzling why deep moisture capture mechanisms were selected in some tropical rainforests in a climate so wet. In a competitive environment, species that unnecessarily allocate a big fraction of fixed carbon to grow roots, at the expense of leaves and branches, would be at a disadvantage when competing against species that concentrated the allocation of carbon above ground (Stephenson *et al.* 2011).

Although extreme evolutionary traits like 18 m deep roots may be unnecessary today, they might have represented an advantage in the past. During the Last Glacial Maximum (21,000 years BP) and until the mid-Holocene (14,000 years BP), the trade winds were more zonal, precipitation rates were lower, and parts of the rainforest were replaced by savannas (Haffer 1969; Van-der-Hammen and Absy 1994; Kubatski and Claussen 1998; Maslin and Burns 2000; Mayle *et al.* 2000). If environmental pressures resulted in the selection of trees with very deep roots to compete for water during the Last Glacial Maximum, it is likely that the climate then also had a strong interannual variability. Dry periods may have been long enough to require deep roots (several years), followed by long wet periods that would recharge the soil. Under such a climate, deep roots may have represented a decisive trait for the survival of tropical trees (Kleidon and Lorenz, 2001).

Mechanisms like deep root development, plant hydraulic uplift, and leaf regeneration in the dry season suggest that Amazonian forests can be resilient to extreme droughts. With these mechanisms, the rainforest may have access to around 3,000 mm of water stored in a thick soil layer. These mechanisms may not be present in every tropical forest. First, we still do not know if the ability to grow deep roots is limited to a few species or shared by many. Moreover, Canadell *et al.* (1996) report that the average maximum root depth of deciduous tropical forests is only 3.7 m. Besides, the maximum root depth can be geologically limited. For example, in a part of the Guyanas, roots cannot penetrate deeper than a few meters because of less deeply weathered rocks (Brouwer 1996, p.22).

Despite these uncertainties, Singh *et al.* (2020) were able to map root zone storage capacity and cross-analyze them against transects of tree cover along the rainforest-savanna border in South America. Their results indicate that currently, parts of the Amazon rainforest have access to up to 800 mm of stored water in the root zone, although local measurements suggest higher values (see above). They conclude that rainforest species invest in their rooting strategy and modify aboveground allocation in response to water stress. These responses are focused on allocating carbon in the most efficient way possible to maximize hydrologic benefit.

7.2.2.2 The biotic pump and the role of the forest in the onset of the rainy season

The forest's fundamental role in regional moisture transport and balance has been discussed in the context of the biotic pump theory. This theory suggests that atmospheric condensation of water vapor supplied by plant transpiration from forests is a mechanism that not only contributes to recycling of rain (as described in section 7.2.1 above), but also exerts a major influence over atmospheric dynamics (Makarieva and Gorshkov, 2007; Makarieva *et al.* 2013). Specifically, re-condensation of the forest’s evapotranspired water is a mass removal of water from the gas phase that induces a decline in air pressure in the lower atmosphere, with consequent horizontal pressure gradients that accelerate air motion. ET-supplied water vapor thus provides a store of potential energy available to drive additional winds (beyond what would be expected from the general atmospheric circulation) that then contribute to the transport of ocean-evaporated water vapor to continental forests. There is a debate about whether this is a fundamentally different theory or another perspective on classic atmospheric circulation theory, differing in the role of internal versus external sources of water vapor (Meesters *et al.*, 2009; Makarieva and Gorshkov, 2009; Makarieva *et al.* 2014; Makarieva *et al.*, 2017; Jaramillo *et al.*, 2018). In any case, this theory has been increasingly adopted in the literature to explain the exponential increase of rainfall over forested areas of the Amazon (Poveda *et al.* 2014; Sheil, 2018; Molina *et al.* 2019).

Closely related to the biotic pump is the concept that high water fluxes from rainforest transpiration during the dry season stimulate an earlier return of wet season rains than would be expected from atmospheric dynamics alone (Wright *et al.* 2017). Specifically, rainforest transpiration increases shallow convection that moistens and destabilizes the atmosphere during the initial stages of the dry-to-wet season transition, conditioning the regional atmosphere for a rapid increase in rain-bearing deep convection. In turn, this process drives moisture convergence and wet season onset 2–3 months before the arrival of the Amazon Convergence Zone. Recent evidence using both rain gauge and the Tropical Rainfall Measuring Mission (TRMM) data empirically demonstrates the role of rainforests in several critical features of the Southern Amazon rainy season. Leite-Filho *et al.* (2020) have shown that forests' presence is associated with an earlier onset and later end of the rainy season, leading to a longer rainy season. Moreover, Leite-Filho *et al.* (2019) have shown that higher forest cover is associated with a low frequency of dry spells of any duration in September, October, April, and May, the transition months between the dry and rainy seasons. In other words, in well-preserved areas, the rainy season begins earlier and is less likely to be interrupted by a long dry spell in its initial days. On the other hand, in heavily deforested areas, the rainy season starts late and is more likely to be interrupted.

Observational studies of Spracklen *et al.* (2012) confirm the dependence of rainfall amounts on the cumulative exposure of 10-day air back-trajectories to vegetation leaf area index (LAI). They used satellite remote-sensing data of tropical precipitation and LAI, combined with simulated atmospheric transport patterns, and concluded that air that has passed over extensive vegetation in the preceding 10 days produces at least twice as much rain as air that has passed over little vegetation. This empirical correlation is consistent with ET maintaining atmospheric moisture in air that passes over extensive vegetation.

These mechanisms imply active, positive feedback. The amount of forest cover regulates the amount and timing of precipitation received by those forests, with forest loss/increase leading to reductions/increases in rainfall and subsequent further impacts on forest cover (see also discussion on Chapter 21).

7.2.3 The role of the forest as a source of water vapor to other regions

The Amazon region is also an important source of moisture for several regions of South America, such as providing moisture and rainfall to glaciers in the Andes, paramos, major cities, and the La Plata River Basin (Marengo *et al.* 2004, Arraut *et al.* 2012; Zemp *et al.*, 2014; Drumond *et al.*, 2014; Poveda *et al.*, 2014; Gimeno *et al.* 2019). Over the La Plata River Basin, and possibly over the Pantanal (wetlands in Brazil) and Andean regions, the Amazon is the second-highest continental contributor to annual mean precipitation (Martinez and Dominguez, 2014), with local recycling over the La Plata Basin being the main source. This water vapor transport happens in relatively narrow spaces of the atmosphere nicknamed “aerial rivers” (Box 7.1). Moreover, external sources from the southern Pacific and Tropical Atlantic oceans also contribute to precipitation in the basin (Drumond *et al.*, 2008). Drumond *et al.* (2008) highlighted that the influence of the tropical Atlantic Ocean varies seasonally from the northern regions in the austral summer months (Martinez and Dominguez, 2014).

The southwestern part of the Amazon basin is an important direct source of incoming moisture over the La Plata Basin, the Andean Amazon, and the Pantanal regions all year round. Water from the Amazon is exported out of the basin and transported via the South American Low-Level Jet (SALLJ) along the Andes (Marengo *et al.* 2004, Drumond *et al.*, 2008, 2014; Arraut *et al.* 2012; van der Ent *et al.*, 2010, Poveda *et al.*, 2014). This warm-season regional circulation feature represents a nucleus of strong low-level winds (See Chapter 5, Section 5.2) in the middle of moisture transport by the trade winds coming from the tropical Atlantic ocean. This system transports and distributes moisture from the entire Amazon Basin into the La Plata Basin and the Andean Amazon region, producing rainfall, as well as over the Pantanal and the agricultural lands of west-central Brazil. Moisture transport associated with SALLJ and the role of the LLJ east of the Andes in precipitation events that occasionally lead to extreme precipitation and major floods are discussed in studies such as Gimeno *et al.* (2016, 2019) and Marengo *et al.* (2020). This system also transports smoke and aerosols from biomass burning in the Amazon to adjacent regions favoring atmospheric pollution over cities in those regions (Mendez-Espinosa *et al.*, 2019).

7.3 Climate regulation provided by the forests

7.3.1 Temperature regulation

Why are Amazonian forests much cooler than the land uses that often replace them? The answer to this question is crucial to understanding the Amazon's capacity to provide ecosystem services and how this capacity may diminish with deforestation, forest degradation, and global climate change (Foley *et al.* 2007, Coe *et al.* 2016). Recent studies on land surface temperature regulation indicate that Amazonian forests act like giant air-conditioners (Silvério *et al.* 2015, Coe *et al.*, 2017). This characteristic relates primarily to forests' ability to cycle large amounts of water vapor from the soil to the atmosphere via ET (Nobre *et al.*, 2016) (see previous sections). Compared with most crops cultivated in the region, Amazon forests have rougher canopies, denser canopy cover throughout most of the year, deeper roots, and an overall higher capacity to absorb solar energy and return it back to the atmosphere overwhelmingly as latent heat (Coe *et al.* 2016). Combined with the high net surface radiation and precipitation inherent to the region, these characteristics result in a disproportional capacity of forests to cool down their leaves. For instance, the daytime land surface temperature in forested areas of the southeastern Amazon tends to be 5ºC lower than deforested areas during the dry season, a result of ET decreasing, on average, by a third as forests are replaced by pastures and croplands (Silvério *et al.* 2015).

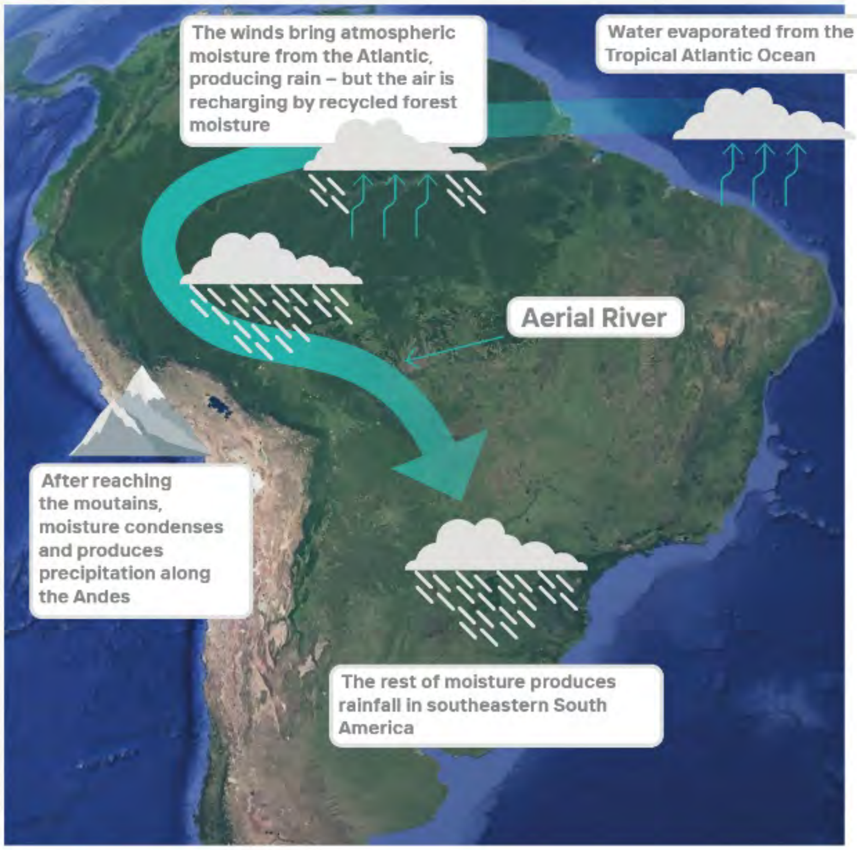
The relatively cool surface of Amazon forests relates to complex interactions between biological, physical, and chemical processes (Still *et al.*, 2019). Most Amazonian tree species prevent leaf temperatures from increasing above critical levels, which can avoid overheating and associated reductions in carbon assimilation, growth, and carbon storage, all of which influence the odds of plant survival (Brando *et al.*, 2019). Some studies suggest that the optimal temperature for leaf photosynthesis is less than 30°C, with leaf photosynthesis dropping abruptly when temperatures rise above 35ºC (Doughty and Goulden 2008), though there is debate about whether the mechanism of photosynthesis limitation is temperature or associated vapor pressure deficit (Smith *et al.* 2020). A recent long-term study found that South America's rainforests carbon stocks and carbon gains decrease significantly ($P < 0.001$) with the mean daily maximum temperature in the warmest month (Sullivan *et al.* 2020). This process helps to explain why the average surface temperature of Amazonian forests is usually below 30ºC (Coe *et al.*, 2016). While ET controls much of this capacity to regulate surface temperatures, other foliar characteristics contributing to leaf cooling include leaf angle, size, shape, and pubescence; canopy position; number of leaves per stem; and canopy structure (Brando *et al.* 2019).

ET and land surface temperatures appear to be relatively constant across the Amazon Basin. Yet, there are important finer-scale spatial and temporal variability in canopy properties, ET, and land surface temperature. The main environmental process controlling this spatial variability is solar radiation (Fisher *et al.*, 2009). Although potential incoming shortwave radiation is high across the entire region, some portions of the Amazon (e.g., near the Andes) receive less radiation due to cloudier conditions than others (the southeastern Amazon). The second factor relates to soil water availa-

Box 7.1 Aerial rivers

In recent years the term atmospheric river has evolved and is now established as describing a narrow band of atmospheric moisture, usually originating from the tropics, making landfall in the mid-latitudes. Low-level jets (LLJs) are defined as regions of anomalously high wind speeds occurring within the first kilometer of the troposphere (see Section 5.2, Chapter 5). In the case of the Amazon Basin, these columns of vapor move with the weather, carrying an amount of water vapor roughly equivalent to the average flow of water at the mouth of the Amazon River (Arraut *et al.* 2012), and are referred as aerial rivers, a nick name for the South American LLJ east of the Andes (SALLJ).

When the atmospheric rivers make landfall, they often release this water vapor in the form of rain. The figure shows a schematic representation of moisture transport in the Amazon region. Moisture evaporated from the Atlantic Ocean is carried by surface winds into the region, with stronger transport along the SALLJ. The winds get even more humidity from the moisture recycling provided by the forest. The moist air first moves westward, but as it approaches the eastern flank of the Andes, it is deflected toward southeastern South America, generating the SALLJ. This moisture transport is like a river in the air that brings moisture and rain to the southern Amazon, Pantanal, and the La Plata Basin, with the SALLJ the core of the river (Arraut *et al.* 2012). That is why this transport is referred to as "aerial rivers" over land, where the moisture flow is in the form of water vapor and clouds.



Source: Rios Voadores project: www.riosvoadores.com and Marengo 2020.

bility. Where there is an intense dry season (or in extremely dry years like the 2015-2016 El Niño event), low soil water availability towards the late dry season can constrain ET and cause related increases in land surface temperature (Gimenez *et al.* 2019). In the southeastern basin, where the dominant land cover is cerrado (mainly savannas), dry season ET may be less than half of that of the wet season (Costa and Pires 2010), with surface temperatures increasing proportionally to decreases in ET during the late dry season. Similarly, when soil moisture drops below critical levels during drought years, plant water stress can trigger reductions in stomatal conductance and ET, resulting in increased land surface temperatures (Toomey *et al.*, 2011). Thus, while the climate over much of the Amazon is adequate for plants to maintain high ET and associated cooler temperatures, broad patterns across the region exist.

Air temperature and land surface temperature, although with the same tendency, often differ, with differences between them resulting from differences in the specific heat values of air, soil, and water, and from complex interactions among atmospheric properties, soil moisture, net radiation, and elevation. In general, air and land surface temperatures converge to similar values during the night but diverge during the hotter parts of the day, when land surface temperatures usually surpass air temperature by several degrees (Still *et al.*, 2019). As large tracts of Amazonian forests are deforested, we expect major increases in surface temperatures (Silvério *et al.*, 2015), given that deforestation results in decreased ET. This warming can be larger than the cooling effects that deforestation causes by increasing albedo.

7.3.2 Edge effects on temperature and moisture

More than 70% of the world's remaining forest is less than 1 km from an edge (border adjacent to a field), and 20% is less than 100 m from an edge (Haddad *et al.*, 2015). In human-dominated tropical landscapes, forest edges and their effects are pervasive (Skole and Tucker 1993, Pfeifer *et al.* 2017). As people clear-cut forests to expand pastures, croplands, and palm oil plantations, associated changes in disturbance regimes and the regional energy balance can degrade much of the residual forest. Thus, we expect additional carbon losses for each hectare deforested, especially along forest edges neighboring agricultural fields. In the 'arc of deforestation' in the southeastern Amazon, nearly 14% of Amazonian forests now grow less than 100 m from a deforested area (Brando *et al.*, 2014).

Forest edges adjacent to cleared fields are subject to prolonged forest degradation. These edges and forest patches are exposed to hotter, dryer, and windier conditions (Didham and Lawton 1999, Schwartz *et al.* 2017). These edge effects degrade forests over time and have important implications for forest structure, especially because they tend to disproportionately increase mortality of canopy dominant trees over the short-term (Laurance *et al.* 2000). The resulting changes in microclimate then facilitate the establishment of light-wooded (low wood density), small-sized, fast-growing pioneer species (Laurance *et al.* 2002), causing regional reductions in forest carbon stocks over the long-term (Chaplin-Kramer *et al.*, 2015, Silva Junior *et al.*, 2020).

Tropical forests are highly resilient to occasional disturbances, but increased frequency or intensity of disturbance events are expected to dramatically change forest structure, composition, and function (Brando *et al.* 2014, Lewis *et al.*, 2015, Nobre *et al.*, 2016). When combined with climate change, these disturbances may outpace adaptation processes (Lewis *et al.* 2015, Trumbore *et al.*, 2015). The combined effects of continued deforestation and a changing climate place large areas of the Amazon at risk of greater degradation in the coming decades (Maxwell *et al.*, 2019), particularly along forest edges neighboring deforested fields and in isolated forest patches (Gascon *et al.* 2000, Matricardi *et al.*, 2020).

Quantifying the drivers of forest degradation in the Amazon (see Chapter 19) is key to developing, validating, and parameterizing Earth system models (ESM) that mechanistically simulate changes in carbon pools and fluxes between the biosphere and atmosphere (Rödig *et al.* 2018). Advances in mapping forest degradation and its drivers have permitted substantial improvements in ESMs' ability to project potential pathways of Amazonian forests. However, very few (if any) of these new advancements have addressed the issue of forest edge degradation. Hence, projecting the future of Amazonian forests requires a better representation of forest edge effects in ESMs.

7.4 Conclusions

Internal biogeophysical processes strongly control the hydrological and climate system of the Amazon Basin. This is possible because several mechanisms to access water stored in deep soil layers were selected for in rainforest tree species and provide the energy necessary to trigger and maintain convection. These combined mechanisms lead to a more humid climate on average and an earlier start and later end of the rainy season. Simultaneously, they maintain surface air warm enough for instability and convection, but within limits that do not hinder the photosynthetic capacity of the trees.

Such mechanisms, along with the microclimate temperature and humidity control at the edges of the forest, are fundamental features of the coupled biosphere-atmosphere system in the Amazon, helping define the Amazon's climate and the climate in other parts of South America. Moreover, these mechanisms ensure this coupled system's ability to endure the dry season along its southern borders and provide a steady source of water vapor to the Amazon's atmosphere when inputs from the Atlantic ocean weaken.

7.5 Recommendations

Forest cover regulates the amount and timing of precipitation received by those forests, with forest loss/increase leading to reductions/increases in rainfall and subsequent further reductions in forest cover. If the rainforest is replaced with another land cover, the Amazon would have a hotter climate and would not maintain ET at the same rate, particularly during the dry season, changing rainfall amounts and decreasing the duration of the rainy season, with implications for forest degradation, forest flammability, and crop yields.

The most important changes in the hydroclimate system are happening in the transition between the dry and the rainy seasons, with a lengthening of the dry season, which has important consequences to ecosystem ecology, surface hydrology, and intensive agriculture in the region. In particular, the lengthening of the dry season makes the climate more seasonal – a tropical savanna climate instead of a tropical rainforest climate. Future biosphere-atmosphere interaction studies should focus on these particular seasons.

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Amazon Assessment Report 2021

Chapter 8

Peoples of the Amazon before European Colonization

O cacique Adílio Kanamari , cujo nome na sua língua é Arabonã (Foto: Bruno Kelly/Amazônia Real)

INDEX

Graphical Abstract

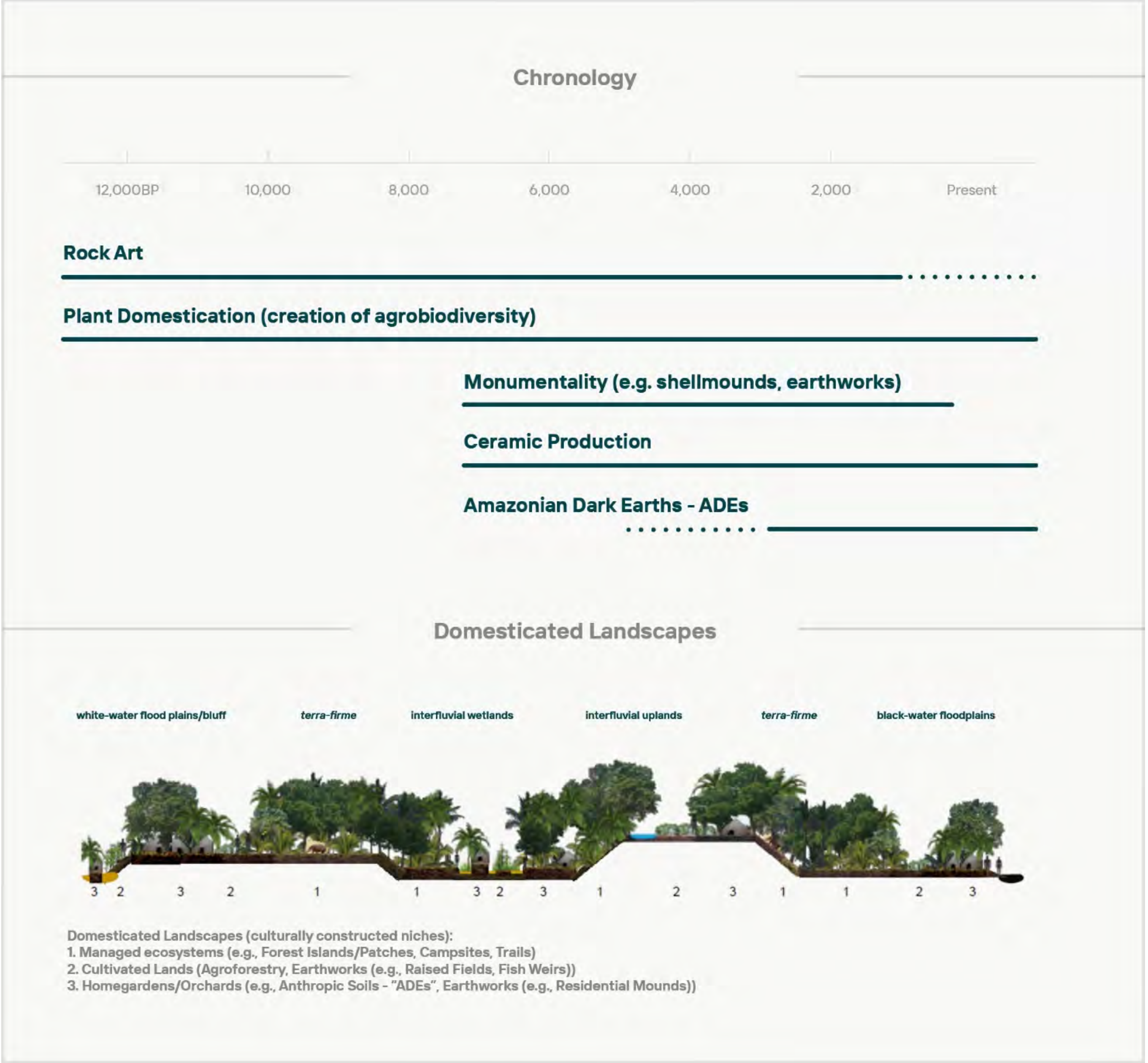

Figure 8.A Schematic representation of landscape transformations associated with the history of Indigenous occupation of the Amazon. Management practices and plant domestication intensifies with greater proximity to residential locations. (Source: Carolina Levis).

Peoples of the Amazon before European Colonization

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Key Messages

- The Amazon has been occupied by Indigenous people for over 12,000 years.
- During this long history, Amazonian Indigenous societies developed technologies that were highly adapted to local conditions and which optimized their development and the expansion of food production systems, including anthropic soils, raised fields, and agroforests.
- Such technologies have long-lasting impacts which are incorporated into contemporary Amazonian landscapes.
- These technologies can inspire new forms of urbanism, waste management, and land-use systems highly integrated with the Amazon's natural conditions, with the potential to boost sustainable solutions for Amazonian development.
- Amazonian archaeology shows how the early Indigenous history of the region is characterized by the production of cultural and agrobiological diversity.
- The Amazon was a major focus of cultural and technological innovation in South America. It is one of the world's few independent centers of plant domestication, and home to the earliest ceramics production in the Americas.
- The evolutionary history of Amazonian Biomes during the Holocene was significantly affected by Indigenous peoples' management practices.
- Strict-protection nature reserves whose interiors have been traditionally occupied should be reconfigured to allow traditional peoples to remain and continue their ways of life, preserving their natural-cultural heritage.
- Society at large must be made aware of the fundamental intellectual contributions of Amazonian peoples to both national and global development

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Abstract

Indigenous occupation of the Amazon started around 12,000 years ago. Archaeological evidence shows that these early settlers already exhibited cultural diversity, expressed in different rock art styles and stone artifacts. These early societies had diversified economies that included generalized consumption of different plants and animals, together with the early cultivation of plants. Such practices of plant cultivation transformed the Amazon as one of the independent centers of plant domestication in the world, as well as a cradle for the production of agrobiodiversity, embedded in systems of knowledge still kept by Indigenous and other traditional societies in the present. The Amazon was also a cradle for other cultural innovations, such as the production of the earliest ceramics in the Americas, early monumental architecture, and the dark fertile soils known as "*terras pretas*". Along this long history one sees the continuous expression of cultural differentiation manifested, for instance, in distinct ceramic styles with sophisticated iconographies and production technologies, as well as by the impressive number of different languages and families of languages spoken, which rank among the highest in the world. Archaeology tells us how Indigenous peoples transformed nature in the Amazon over millennia to the point that it is hard today to disentangle natural from cultural heritage there. It also shows that any kind of sustainable future has to take into account the rich Indigenous heritage manifested in archaeological sites, contemporary landscapes, and the contemporary knowledge of traditional societies.

Keywords: Archaeology, deep history, forest peoples, landscape domestication, past cultural diversity, natural heritage as cultural heritage, traditional knowledge

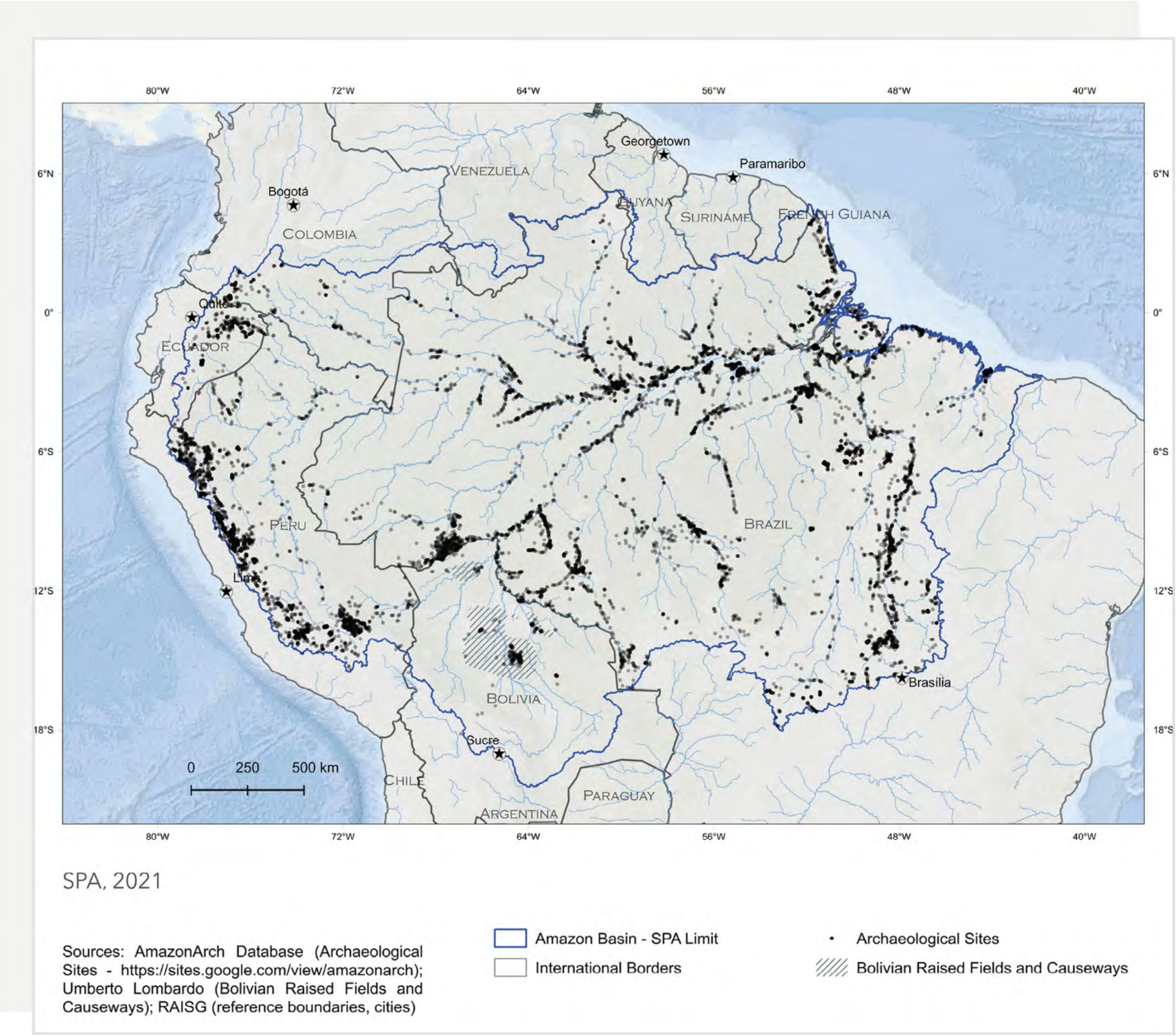
8.1. Introduction

There are a number of ways to learn about the past. Ancient texts, documents, maps, and photographs, for instance, are traditionally considered the staple foods of history. But in the Amazon, the geographic and temporal scope of such sources is restricted to places visited or occupied by Europeans and their descendants; further, such items were often produced by these external actors, whose primary commitment was to the Catholic Church, colonial administrations, or, as the nineteenth century progressed, constructing national identities and/or an emerging ideal of science. In contrast, the oral histories of Indigenous peoples and local communities (IPLCs), based on collective human memory, counteract Eurocentric perspectives, even though many groups suffered demographic collapse after European conquest and colonization, interfering with the transmission of history between generations. Fortunately, contributions by Indigenous intellectuals are now mounting; these reflect on their past and present histories, climate change, and State policies directed at forest areas, among other issues (Kopenawa and Albert 2013; Krenak 2019, 2020; Baniwa 2006; Lima Barreto 2013; Benites 2014; Jacupe 2000). As the coronavirus pandemic has taken the lives of a large number of elders in a short space of time, much of this knowledge is still being lost.

By studying the material remains of human presence and actions, archaeology provides a singular opportunity for understanding the human past from its earliest manifestations up to the present, at several temporal and spatial scales, permitting us to examine continuities and historical processes that could otherwise elude observation (Heckenberger 2005). Interdisciplinary by nature, archaeological investigations can incorporate investigative methods and/or information from the fields of history, anthropology, linguistics, geology, biology, genetics, and ecology, among others, to further its understanding of the past.

Estimates indicate that the Indigenous population of the Amazon today is just a small fraction of what it was on the eve of European invasion (Koch et al 2019). By the sixteenth century, there were roughly 10 million people living in either small semi-permanent settlements or large permanent villages of over 50 hectares (Tamanaha 2018). Thanks to the construction of cultural niches, large populations were achieved without reaching environmental carrying capacity (Arroyo-Kalin and Riris 2020); or in other words, without the over-exploitation of resources.

Archaeological research in the Amazon has increased considerably during the last decades. Academic archaeology gained momentum in the region following the development of large international and interdisciplinary collaborations and the consolidation of Amazon-based research groups and university archaeology departments, all of which have contributed significantly to broadening and deepening our knowledge of the histories of Amazonian Indigenous populations (Figure 8.1). These developments resulted, in part, from an increase in contract archaeology, which expanded substantially in Brazil following a 2002 federal decree requiring archaeological inventories, impact studies, and rescue operations to be completed prior to construction of infrastructure projects. Both in Brazil and in other Amazonian countries,



SPA, 2021

Sources: AmazonArch Database (Archaeological Sites - https://sites.google.com/view/amazonarch); Umberto Lombardo (Bolivian Raised Fields and Causeways); RAISG (reference boundaries, cities)

Figure 8.1 Archaeological sites of the Amazon (Source: AmazonArch).

such archaeological research has revealed thousands of archaeological sites, many of which have been documented prior to their destruction.

In this chapter, we provide a panorama of Amazonian history that stretches back at least 12,000 years. Although biased towards Brazil, where there is comparatively more research, we aim to bring in data from other Amazonian countries. Although found in the Amazon Basin, interesting and important archaeological sites and cultures, such as Machu Picchu and Chachapoyas (Kuelap) in Peru, or Samaipata in Bolivia, were not included because of their clear connection with the Andes, as well as lack of space.

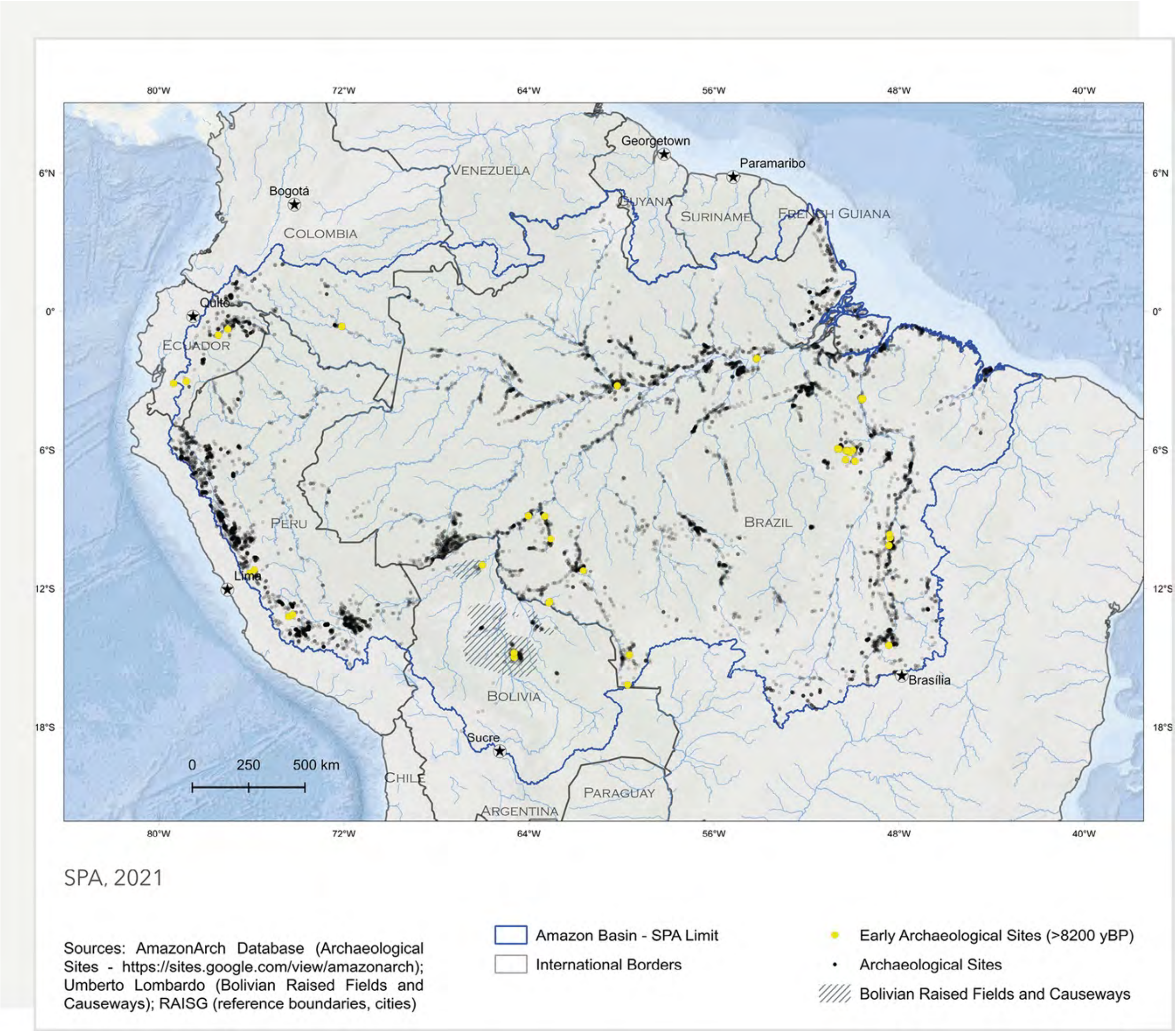
We demonstrate how the region's human history is closely interwoven with important environmental transformations that affected the distribution of vital resources today. In this way, we introduce Amazonian peoples' remarkable cultural achievements and the deep history of their impressive linguistic and cultural diversity. To do this, we will employ certain concepts that we present below. Towards the end of the chapter, we consider how archaeology in the Amazon is alive and undertaken by IPLCs, and provides a privileged route to understand the history of the region from the distant past to the recent present. Although the focus of this chapter falls mostly on the periods prior to 1492, we aim to show that archaeology is an invaluable tool to assess the application of policies that affect IPLCs' territories. This leads us to recommendations for policy makers at the end of the chapter.

8.2. Initial Settlement of the Amazon

In the late 1980s, it was proposed that tropical rainforests could not have been occupied by hunter-gatherer groups before the advent of agriculture (Headland 1987; Bailey *et al.* 1989). It was also proposed that Amazonian hunter-gatherer societies today were descended from farmers that settled along the major rivers after being expelled from these areas to the hinterlands, resulting in the abandonment of farming due to environmental pressures (Lathrap 1968). The notion that environmental hostility and forces of nature triggered a process of decay in Amazonian populations goes back to the early 19th century and influenced the first archaeological research conducted in the mid-20th century. The high visibility of archaeological sites containing elaborate ceramics and monumental structures prompted suggestions of a late arrival of humans to the Amazon from more culturally 'advanced' areas, such as the Andes. These reconstructions have been falsified by data from diverse Amazonian regions that evidence human settlement since the Terminal Pleistocene, well before the advent of farming.

Records of these first colonists are still relatively scarce due to the fact that some of their settlements are either buried under meters of sediment or were carried away by fluvial erosion. To date, at least sixteen sites from the Terminal Pleistocene and Early Holocene have been recorded, especially in Brazil and Colombia (Figure 8.2). The archaeological evidence shows that at the Terminal Pleistocene and early Holocene (15,000-8,200 BP), small groups settled in rock shelters, whose walls are normally covered with paintings (See Box 8.1). From the outset, there was no single cultural tradition that could be associated with these early occupations, at least based on the lithic (stone tool) artefacts found at these sites. In the upper Guaporé Basin, the Abrigo do Sol rock shelter yielded radiocarbon dates between 14,700 and 8,930 BP (Miller 1987: 63-4), associated with a diversified unifacial lithic assemblage. Lithic remains from Pedra Pintada cave, in the lower Amazon region, yielded bifacial lithic artefacts dating to c. 11,200 BP (Roosevelt et al. 1996). At Cerro Azul, in the middle Guaviare River, in Colombia, lithic remains dating back to 10,200 BP were reported in an area with rock art of potentially the same age (Morcote-Ríos et al. 2020; Box 8.1). In Llanos de Mojos, Bolivia, there is evidence of Indigenous occupation and plant cultivation at 9,420 BP (Lombardo et al. 2020). In the middle Caquetá River, also in the Colombian Amazon, open-air sites of Peña Roja and San Isidro produced unifacial lithics dating to c. 9,000 BP (Gnecco and Mora 1997). In the Carajás hills of Pará, Eastern Amazonia, an unifacial lithic tradition found in rock shelters has been dated to c. 8,800 years BP (Magalhães 2016). In the upper Madeira Basin, there is a long record of production of unifacial lithic tools and flaked axes dating back to the early Holocene (Miller et al. 1992). In much of the Amazon, the availability of stone suitable for the manufacture of tools is unequal. This possibly led to a rapid dispersion of populations in search of these resources, and, at the same time, boosted other technological alternatives and strategies in the vast expanses where these resources were not available.

Faunal remains are found together with stone tools, including those of small- and medium-sized mammals, fish, reptiles, birds, and gastropods. Plant remains include palm fruits, legumes, and other fruit trees. In contrast to material culture differences, one notices a broad-spectrum dietary patterns among these popular-tions, contrary to some other places in the Americas where early settlers adopted specialized strategies. The high diversity of biomes within the Amazon was likely one of the drivers for the emergence of cultural diversity among the early settlers, establishing early on a pattern that prevailed throughout the Holocene.



Sources: AmazonArch Database (Archaeological Sites - https://sites.google.com/view/amazonarch); Umberto Lombardo (Bolivian Raised Fields and Causeways); RAISG (reference boundaries, cities)

Figure 8.2 Terminal Pleistocene and Early Holocene Archaeological sites of the Amazon (source AmazonArch)

Box 8.1 Ancient Amazonian Rock Art

Rock art is the most ubiquitous manifestation of humankind's early history and is found all over the world but Antarctica. The oldest known paintings of recognizable objects go back to 45,500 years to paintings representing pigs found in a cave in Sulawesi, Indonesia (Brumm et al. 2021). Older records of abstract paintings are found in caves in Spain associated with neandertal occupations dating to 64,000 years (Hoffmann et al. 2018). Rock art sites are widespread all over the Amazon and some of them seem to be contemporary with initial occupation of the area.

Amazonian rock art was produced with two basic sets of techniques: painting and engraving (Pereira 2017). Engravings, also known as petroglyphs, are the most common type of rock art in the Amazon, and were produced by techniques that included scraping, fine-line and deep incisions, and picking. Petroglyphs are found in rocky outcrops along river rapids and falls and also in rock shelters and caves. The strong correlation between petroglyphs and rapids increases their archaeological visibility (Pereira 2017). Paintings were prepared with pigments made of natural minerals, such as iron oxide for red and yellow, carbon and manganese for black, and kaolin for white. These were pulverized and mixed with gelatinous bases made of organics such as resins, eggs, fat, and water. Paintings are normally found on exposed boulders, rock shelters, or caves, in the latter case in places away from and above water bodies.

Rock art sites are difficult to date with standard archaeological techniques. The establishment of the ages of petroglyphs is almost impossible at the moment, since engravings leave no organic trace that can be radiocarbon dated. Likewise, the organic materials that were mixed with pigments are normally found in trace levels, hindering the establishment of secure radiocarbon dates. Consequently, one form of dating paintings is to establish the age of carbonate crusts that grow on the top of them, or to date buried strata that have fallen blocks of painted rock embedded in them. Despite these shortcomings, some of the best-known manifestations of painted rock art from the Amazon come from places where the earliest secure evidence of Indigenous occupation is found; La Lindosa and Chiribiquete, in Colombia, and Monte Alegre, in Brazil (Morcote-Ríos et al. 2020; Roosevelt et al. 1996).

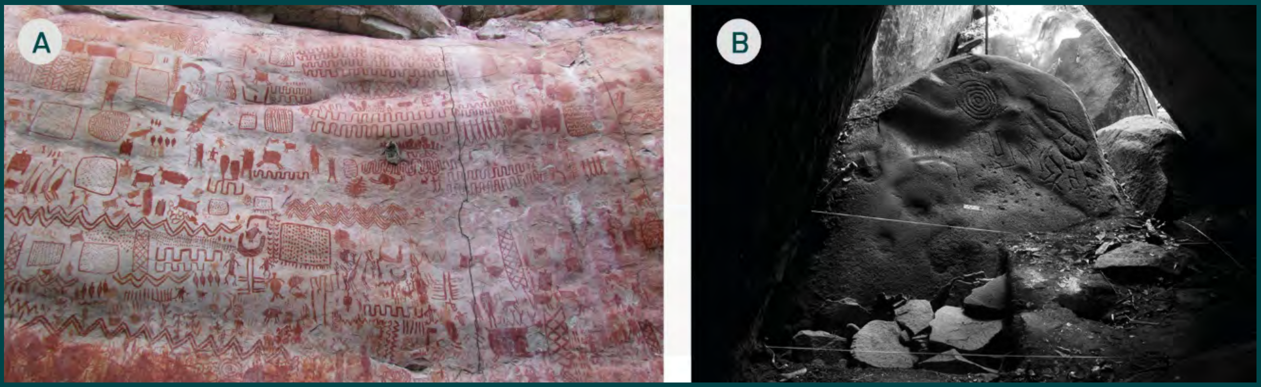


Figure 8.B1 A) Panel with zoomorphic, anthropomorphic, and geometric motifs dating from the Pleistocene/Holocene transition, Cerro Azul rockshelter, Guaviare river, Colombia (photo credit Gaspar Morcote-Ríos); B) Panel with geomoetric motifs (ca. 4,000 BP) Arara Vermelha site, Roraima, Brazil (credit Marta S. Cavallini)

In the now remote area of Chiribiquete, spectacular groups of painted motifs cover large areas of rock shelters. Most painting activities date back to 3,500 to 2,500 BP but here are contexts indirectly dated to 19,500 BP (Castaño-Uribe and Van der Hammen 2005). At Cerro Azul, in the Serranía La Lindosa area, a sandstone formation on the Guaviare River, there is tentative evidence of Indigen-

Box 8.1 ***continued***

ous occupation older that 20,000 years, but it is from ca. 12,100 years BP that one sees the onset of stable, repeated human presence (Morcote-Ríos et al. 2020: 6). Among the painted motifs found in this and other sites in the area are realistic depictions of extinct Pleistocene megafauna, such as giant sloth, mastodon, camelid, horse, and macrauchenia. This combination of factors suggests that the paintings date to the Terminal Pleistocene or Early Holocene.

Pedra Pintada (literally "Painted Rock") cave is in a sandstone massif that overlooks the Amazon River floodplain, near the city of Monte Alegre in the Lower Amazon. There, paint spalls on fallen blocks are found in a stratum dated to 11,200 BP (Roosevelt et al. 1996). Not far from the cave, there are beautiful polychrome paintings that were made on an exposed cliff face at Serra da Lua whose age is unknown. Detailed studies of the composition of the panels, the graphic motifs, and the presence of evidence of pigment production found in excavations suggest that rock art permeates the entire history of occupation in the region (Pereira and Moraes 2019). In some cases, the motifs painted on rocks and those on ceramics present striking similarities (Pereira 2010).

Rock art diversity in the Amazon echoes the diversity seen in other archaeological forms. Sites with painting are concentrated in areas far away from each other with their own independent artistic traditions. Petroglyphs, on the other hand, perhaps because many of them are located in rapids or waterfalls, have a more widespread distribution and display recurrent patterns including faces, whole human figures, adornments such as masks, and geometric motifs.

Although difficult to date, there are attempts to correlate petroglyphs in places such as the Caquetá, Negro, and Tapajós Rivers with the mythical narratives of Indigenous people that currently live there, such as the Tukanoans and the Munduruku (Urbina 2004; Valle 2012). Indeed, for many Indigenous people, rock art plays an important symbolic and political role today (Pereira 2017). In the Apaporis River in Colombia, there is the Nyi Rock site, whose engravings are sacred for the local Indigenous groups, as is the case for the Takana regarding the petroglyphs of Beni River, in Bolivia. In Roraima, Brazil, the Macuxi, Wapishana, and Taurepang living in the São Marcos Indigenous Land see a direct connection between local rock art and their ancestors, a fact used to support their territorial claims.

The recent wave of construction of massive hydroelectric power plants poses an immense threat to these sites. Although recorded by preventative archaeological work, petroglyphs have been flooded or literally exploded, as in the Upper Madeira River for the construction of the Santo Antonio dam. The same may also happen if other dam projects go ahead along the Bolivia-Brazil border in the Mamoré River.

This pattern correlates today with the large diversity of langua-ges, around 300, and genetic units (language families and isolated languages), around 50, found in the Amazon (Epps and Salanova 2013). Genetic data show that virtually all Indigenous American populations south of the Arctic Circle share the same genetic background derived from Northeast Asia, and this is the case of Amazonian Indigenous peoples as well (Posth et al. 2018).

8.3. Culture-climate interactions

Scholars sought early on to explain spatial and temporal variability within the archaeological record as a result of past climate and/or environ-mental change. Millennial- and decadal-scale droughts (and associated savanna expansion under the forest refuge hypothesis [Haffer 1969], now rejected [Bush 2017]) were hypothesized to have caused the diversification of Amazonian languages, as well as the rise and fall of different cultures (Meggers 1975, 1993).

Such theories lost favor with the recognition that past and contemporary Indigenous peoples use multiple strategies to overcome environmental constraints. Research programs combining archaeology and paleoecology allow the rethinking of people-climate-environment interactions in the Amazon.

The climate during the Late Pleistocene, when humans first arrived in the Amazon, was ~5°C cooler and, in some places, up to 50% drier than today. Early settlers would have encountered drier forest or savanna vegetation in the more seasonal fringes of the Amazon Basin (Anhuf 2006; Piperno 2011), as well as megafauna, whose extinction (possibly aggravated by human predation) had a myriad of ecological consequences (Doughty et al. 2016). With the onset of the Holocene (11,200 BP), warmer, wetter conditions led to forest expansion, as human populations began increasing at a continental scale (Goldberg et al. 2016).

In the Mid Holocene (8,200-4,200 BP), cooling in the Northern Hemisphere led to changes in the South American Summer Monsoon (SASM), causing droughts in the western Amazon (Baker et al. 2001), a northward shift of the forest/savanna ecotone along the southern fringes (Pessenda et al. 2001), and wetter conditions in the eastern Amazon (Wang et al. 2017). This period is posited to be characterized by a continent-wide downturn in human populations (Riris and Arroyo-Kalin 2019).

Modern SASM parameters established during the Late Holocene resulted in a wetter climate and the expansion of humid evergreen forest, which reached its current southern limit in the Bolivian Amazon as recently as 2,000 years ago (Carson et al. 2014). Southward expansions of Tupi-Guarani-speaking, agroforestry-practicing groups into the La Plata basin between 2,000 and 500 years has also been linked to forest expansion (Noelli 1996; Iriarte et al. 2016).

In the last millennium, drying associated with the Medieval Climate Anomaly (950-700 BP) may have stimulated large-scale upheaval in the archaeological record of the Amazon (De Souza et al. 2019), while the atmospheric CO_2 increase behind global cooling during the Little Ice Age (450-100 BP) is postulated to have been triggered by the conversion of Indigenous settlements into forest after mass depopulation of the Americas following European contact (Koch et al. 2019), though not without controversy (Boretti 2020).

8.4. Transforming nature: The Amazon as a domestication hotspot

Studies of current practices among IPLCs and the biological assemblages that result from them provide archaeologists with clues to how past practices impacted biodiversity (Levis et al. 2017; Loughlin et al. 2018). Current plant communities result from the interplay between natural ecological processes (i.e., evolutionary forces and environmental selection pressures; e.g. ter Steege et al. 2006) and human activities (termed management practices), which together shape plant species' dispersal capacity, local environmental conditions, and biological interactions (Balée 1989a, 1989b, 2013; Clement et al. 2015; Levis et al. 2018).

By culturally constructing their niches, IPLCs have domesticated Amazonian landscapes by increasing food availability near their homes through practices including (1) removing unwanted plants, (2) protecting useful trees throughout their development, (3) attracting animal dispersers, (4) directly dispersing seeds, (5) selecting specific phenotypes, (6) managing fire, (7) cultivating useful plants, and (8) increasing soil fertility and structure such as creating anthropogenic soils and earthworks (Levis et al. 2018). Even relatively small groups with high mobility and a large dependence on gathered plants, such as the Nukak of Colombia, act to increase concentrations of species useful to them around campsites and along trails, creating resource patches within their territories (Cabrera et al. 1999; Politis 2007).

Plant use and management by Indigenous peoples began over 12,000 years ago (Box 8.2). Archaeobotanical remains of fruits, seeds, and nuts, especially from arboreal plants such as nance (*Byrsonima* spp.), breadnut (*Brosimum* spp.), pequiá (*Caryocar* spp.), Brazil nut (*Bertholletia excelsa*), and palms (*Acrocomia* sp., *Astrocaryum* spp., *Attalea* spp., *Bactris* spp., *Euterpe* spp., *Mauritia flexuosa*, *Oenocarpus* spp., *Syagrus* spp.) are abundant in the earliest (>10 ka) archaeological sites of the Amazon (e.g. Pedra Pintada, Carajás, Cerro Azul, Peña Roja; Box 8.1) (Lombardo et al. 2020; Mora 2003; Morcote-Rios et al. 2014, 2017, 2020; Roosevelt 1998; Roosevelt et al. 1996; Shock and Moraes 2019). This pattern shows how tree and palm species were highly valued and that the use of plant resources was locally persistent enough to prompt redundant use of locales, resulting in places with high archaeological visibility (Shock and Moraes 2019). The collection, consumption, and discard of certain fruits (and their seeds), and the management practices that are implied by human occupation, such as the creation of mosaics of forested and open areas (Box 8.2), eventually created multi-species forest patches rich in resources and persistent consequences for the structure and function of biological communities. Archaeobotanical assemblages from Early- and Mid-Holocene sites located in transitional or ecotonal regions, e.g. Pedra Pintada (Roosevelt et al. 1996) and Monte Castelo (Furquim et al. 2021) show that different microenvironments were often managed concomitantly.

Genetics also tentatively place the wild ancestors of root/rhizome crops such as arrowroot (*Maranta arundinacea*), canna (*Canna indica*), yams (*Dioscorea trifida*), sweet potato (*Ipomoea batatas*) and leren, as well as squash (*Cucurbita moschata*), in the northern and northwestern peripheries of the Amazon. Leren, squash, and bottle gourd (*Lagenaria* sp.) were cultivated at Peña Roja in the Colombian Amazon by 9,000 BP, and several of these species have been documented in Early Holocene sites throughout the Andes, Caribbean, and Central America (Piperno 2011; Pagán-Jimenez et al. 2015, 2016; Aceituno and Loaiza 2018; Castillo and Aceituno 2014). In the Amazon, as well as in the global tropics overall (Denham et al. 2020), vegetatively reproduced plants with edible roots were among the earliest species cultivated by humans (Neves and Heckenberger 2019). These plants would have thrived in the more open forests in the peripheries of the Amazon during the Pleistocene/Holocene transition, making them an attractive resource to the first human settlers (Piperno and Pearsall 1998). By contrast, maize (*Zea mays*), one of only two indigenous cereals cultivated in the Amazon (the other being American rice; Hilbert et al. 2017), spread into South America from Mexico and was incorporated into food production systems much later (ca. 6,850 BP) (Lombardo et al. 2020). Nonetheless, the domestication of maize continued after its arrival in the southwestern Amazon and resulted in the creation of new landraces (Kistler et al. 2018).

Until now we have evidence of only one domesticated animal in the Amazon, the muscovy duck (*Cairina moschata*), the remains of which are found in Late Holocene sites in the southwestern Amazon (Driesch and Hutterer 2012; Stahl 2005). Other animals may have received care from humans without becoming domesticated; for example, there is extensive documentation of turtle corrals in colonial accounts and archaeological remains of artificial ponds in Marajó island and the Llanos de Mojos (Prestes-Carneiro et al. 2020; Schaan 2010). Late Pleistocene/Early Holocene sites from the Colombian Amazon (e.g., Cerro Azul, (Morcote-Ríos et al. 2017, 2020) demonstrate a broad spectrum of animal consumption, including fish, reptiles, and small mammals. The Middle Holocene record of the Monte Castelo shell mound in the southwestern Amazon shows predominantly fish (80% of the vertebrate taxa), specifically drought-tolerant species adapted to the seasonal drying of the surrounding wetlands (Prestes-Carneiro et al. 2020). Predominant exploitation of diverse aquatic resources is also documented in sites along the Amazon River in the Mid to Late Holocene (e.g., Taperinha and Hatahara) (Prestes-Carneiro et al. 2015; Roosevelt

Box 8.2 Archaeobotanical remains

Plants that human populations utilized in the past can be preserved in the archaeological record in the form of different macro- and microscopic remains. Starch grains and phytoliths can be found adhering to the surfaces of artifacts, while phytoliths and charred plant parts, including seeds and wood, preserve in sediments both within and outside archaeological sites. These proxies originate in different ways; starch grains are left by the use or processing of carbohydrate rich plants (Torrence and Barton 2006), phytoliths are deposited after the plants that produce them decompose (Piperno 2006), and charred remains are created under low oxygen combustion, with higher temperatures selecting for plant parts with greater lignin (Pearsall 2015). Pollen, phytoliths, and charcoal found in lake cores can also be indicative of past resource management practices (e.g., Maezumi et al. 2018; Whitney et al. 2013).

We know based on today's Indigenous peoples that early Amazonians would have had varied diets and material culture in different areas of the Amazon, and thus the plants utilized were not all the same at any given time. Food choices depend upon local customs and the presence of environments where different species grow best. Beyond everyday nutrition, plants are also sought for medicine, psychoactivity, hygiene, construction, artefacts, and magic/ritual purposes (Prance et al. 1987; Noelli et al. 2020). Much of this biodiversity remains to be studied in the archaeobotanical record, which is still heavily biased toward routinely-used plants.

Variation in archaeobotanical assemblages is also influenced by the differential presence, preservation, and taxonomic resolution of each proxy; in general, diagnostic starch grains are limited to storage organs (i.e. roots and tubers) and seeds; phytoliths are more frequent and diagnostic in monocot families, such as grasses and palms, but are either undiagnostic or absent in the majority of woody dicotyledon families; hard fruit pits and seed coats are often represented in charred remains; and pollen is more plentiful from wind pollinated taxa, but only preserves in anoxic conditions. Some of the understudied or under-preserved diversity is found in sites with exceptional preservation outside of the Amazon, as is the case for psychoactive plants found in northern Chile (Ogalde et al. 2009) or the Middle Holocene use of chili peppers on the Pacific coast of Peru (Chiou et al. 2014), while more can be estimated about toxic, entheogenic, and medicinal plants from modern documentation or by chemical techniques such as chromatography (e.g., Miller et al. 2019).

Table 8.1 provides a summary of archaeobotanical data so far available for the Amazon which, given all the above factors, likely represents a very small fraction of the true diversity of species utilized in these sites and in the Amazon in general. The larger diversity of plant families present in Late Holocene sites might reveal an actual pattern, but is likely also the result of a much larger sample size (33 sites, compared to 6 Mid Holocene and 7 Early Holocene sites). Likewise, the apparent dip in diversity in the Mid Holocene is likely a result of sample size, as well as the fact that some Late Pleistocene/Early Holocene sites (e.g., Pedra Pintada and Cerro Azul) have exceptional preservation of carbonized remains. Furthermore, the few root, tuber, and rhizome remains from earlier periods likely reflect the difficulty with which these remains carbonize and are preserved in the archaeological record, as well as the relative lack of starch grain studies from these sites.

Taxonomic identification of archaeological plant remains relies upon anatomical and morphological comparisons with modern plant material, and determining which characteristics are unique to different taxa at the level of plant species, genera, or families. Species absent from reference collections cannot be identified archaeologically. The collection and processing of modern species to create reference collections of phytoliths (e.g., Piperno 2006; Morcote-Rios et al. 2016, 2017; Watling et al. 2020a), starch grains (e.g., Pagán-Jiménez 2015), pollen (Flantua et al. 2015), and charred seeds and fruits (e.g., Silva et al., 2015) is a long and continual process, due to the thousands of species that should compose them. The relatively few collections that exist today for this vast region demonstrate better than anything how

Box 8.2 *(continued)*

Amazonian archaeobotany is still an emerging discipline whose true potential for understanding people-plant relationships has not yet been reached.

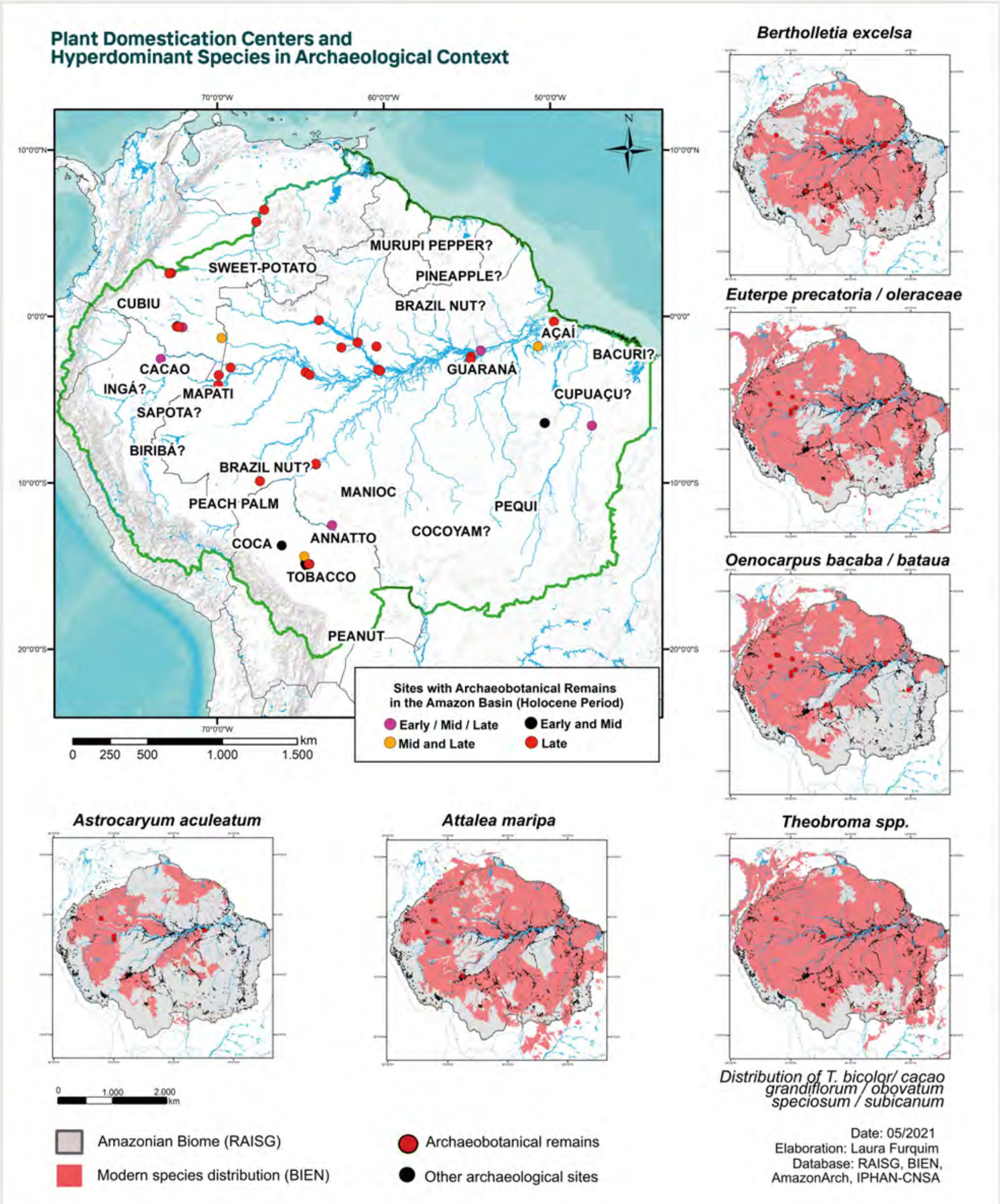


Figure 8.B2 Plant domestication centers and hyperdominant species in archaeological context (drawn by Laura Furquim)

Table 8.1 Food plants recovered from archaeological sites in Amazonia during the Early, Middle, and Late Holocene.

	Late Pleistocene/Early Holocene (12,000-8,200 BP)	***Middle Holocene (8,200-4,200 BP)***	***Late Holocene (4,200-500 BP)***
	7 sites *(Isla Manechi, Caverna da Pedra Pintada, Cerro Azul, Peña Roja, Bacabal 1, Capela, Teotonio)*	***7 sites*** *(La Chacra, Isla del Tesoro, Teotonio, Monte Castelo, San Pablo, Abeja)*	***50 sites*** *(Abeja, Abrigo del Valle de las Piramides, Abrigo Arco, Abrigo Bernardo, Abrigo Selva, Calicata, Campo España, Campo Esperança, Caverna da Pedra Pintada, Cedro, Cerro Azul, Chacra Teleria, Claudio Cutião, Conjunto Vilas, Curare, El Cerro, El Circulo, Fazenda Iquiri, Finca Buenavista, Finca Limoncillos, Floresta, Hatahara, JK geoglyph, La Sardina, Lago das Pombas, Lago do Limão, Las Palmeras, Loma Bella Vista, Loma Mendoza, Loma Salvatierra, Maicura, Mangos del Parguaza, Meseta Araracuara, Monte Castelo, Ome, Parmana, Penã Roja, Porto, Pozo Azul Norte-1, Santa Paula, São João, Serra do Maguari, Sol de Maio, Takana, Teotônio, Tequinho, Tucumã, Tumichucua, Vila Nova I, Vila Nova II)*
Fruits and nuts	*Families: 10; Genera: 11*	*Families: 6; Genera: 6*	*Families: 19; Genera: 27*
	Families: Annonaceae, Cannabaceae, Caryocaraceae, Humiriaceae, Lamiaceae, Lecythidaceae, Malpighiaceae, Memecylaceae, Myrtaceae, Sapindaceae	*Families: Annonaceae, Cannabaceae, Caryocaraceae, Humiriaceae, Lecythidaceae, Malphighiaceae*	*Families: Anacardiaceae, Annonaceae, Cannabaceae, Caryocaraceae, Chrysobalanaceae, Dilleniaceae, Humiriaceae, Lamiaceae, Lauraceae, Lecythidaceae, Malpighiaceae, Malvaceae, Memecylaceae, Moraceae, Myrtaceae, Passifloraceae, Polygalaceae, Sapindaceae, Solanaceae*
	Popular plants: Brazil nut, pequiá, murici, guava, pitomba	*Popular plants: Brazil nut, pequiá, murici*	*Popular plants: Brazil nut, pequiá, murici, cashew, cacao, chili pepper, passion fruit, hog plum, pitomba, uxi*
	Proxy: carbonized seeds	*Proxy: carbonized seeds; phytoliths*	*Proxy: carbonized seeds, phytoliths, starch grains*
Legumes (Fabaceae)	*Genera: 3*	*Genera: 1*	*Genera: 6, Species: 8*
	Genera: Hymenaea, Parkia, Phaseolus/Vigna	*Species: Phaseolus sp. (Common bean)*	*Genera: Arachis, Canavalia, Hymenaea, Inga, Parkia, Phaseolus/Vigna*
	Proxy: carbonized seeds	*Proxy: starch grains*	*Proxy: carbonized seeds, pollen*
Palms (Arecaceae)	*Genera: 8, Species: 15*	*Genera: 6, Species: 6*	*Genera: 14, Species: 29*
	Genera: Acrocomia, Astrocaryum, Attalea, Bactris, Euterpe, Mauritia, Oenocarpus, Syagrus	*Genera: Astrocaryum, Attalea, Euterpe, Lepidocaryum, Mauritia, Oenocarpus*	*Genera: Acrocomia, Astrocaryum, Attalea, Bactris, Chamaedorea, Euterpe, Geonoma, Iriartea, Lepidocaryum, Manicaria, Mauritia, Mauritiella, Oenocarpus, Syagrus*
	Popular plants: babassu, açaí, tucumã, bacaba, bataua, buriti, inajá	*Popular plants: bacaba*	*Popular plants: tucumã, inajá, peach palm, açaí, buriti*
	Proxies: carbonized endocarps or seeds, phytoliths	*Proxies: carbonized endocarps or seeds, phytoliths, pollen*	*Proxies: carbonized endocarps or seeds, phytoliths*

Squashes/gourds	*Genera: 2*	*Genera: 1*	*Genera: 2*
(Cucurbitaceae)	*Cucurbita, Lagenaria*	*Cucurbita*	*Cucurbita, Lagenaria*
	Proxy: phytoliths	*Proxy: phytoliths*	*Proxy: carbonized fruit, phytoliths, starch*
Roots/tubers	*Families: 3, Genera: 3*	*Families: 3, Genera: 3*	*Families: 6, Genera: 8*
	Families: Araceae, Euphorbiaceae, Marantaceae	*Families: Euphorbiaceae, Marantaceae*	*Families: Araceae, Convolvulaceae, Dioscoreaceae, Euphorbiaceae, Icacinaceae, Marantaceae*
	Popular plants: manioc, leren, cocoyam	*Popular plants: manioc, leren, cocoyam*	*Popular plants: sweet potato, yam, manioc, leren, arrowroot, mairá potato, cocoyam*
	Proxy: phytoliths, starch	*Proxy: phytoliths*	*Proxy: carbonized seeds, phytoliths, starch*
Grains (Poaceae)	*Genera: 0*	*Genera: 2*	*Genera: 2*
		Zea mays, Oryza sp. (maize, rice)	*Zea mays (maize), Oryza sp. (rice)*
		Proxy: phytoliths	*Proxy: carbonized seeds, phytoliths, starch*
Other/multiple uses	*Families: Heliconiaceae, Marantaceae, Moraceae, Solanaceae, Strelitziaceae, Zingiberaceae*	*Families: Heliconiaceae, Marantaceae*	*Families: Annonaceae; Asteraceae, Boraginaceae, Burseraceae, Euphorbiaceae, Heliconiaceae, Humiriaceae, Marantaceae, Marcgraviaceae, Melastomataceae, Moraceae, Phytolaccaceae, Solanaceae, Strelitziaceae, Urticaceae, Zingiberaceae*
	Proxy: carbonized seeds, phytoliths	*Proxy: phytoliths*	*Proxies: carbonized seeds, phytoliths*

Source: Data compiled from: Andrade 1986; Arroyo-Kalin et al., 2019; Bozarth et al. 2009; Cascon & Caromano 2012; Cassino 2018; Castaño-Uribe and Van der Hammen 2005; Dickau et al. 2012; Félix 2019; Furquim 2018; Herrera et al. 1980-1; Hilbert 2017; Hilbert et al. 2017; Lombardo et al. 2020, Kosztura-Nuñez 2020; Maezumi et al. 2018; Magalhães et al. 2019; Mora 2003; Mora et al. 2001; Morcote-Rios 2008; Morcote-Rios & Sicard 2009; Morcote-Rios et al. 2013, 2014, 2017, 2020; Pärssinen et al., 2020; Perry 2004, 2005; Roosevelt 1998, 2000; Roosevelt et al. 1996; Piperno 2011; Piperno & Pearsall 1998; Shock in preparation; Shock and Moraes 2019; Alves 2017; Watling et al. 2015, 2018, 2020b.

et al. 1991). Mammals were differentially exploited across the basin, with some species gaining importance in certain areas at particular times (e.g., brocket deer at Loma Salvatierra, Bolivia; Driesch and Hutterer 2012).

By changing the morphology, demography, and distribution of both plant and animal species through their management practices, Indigenous peoples increasingly transformed local ecosystems during the Holocene, domesticating different environments such as forests, savannas, and wetlands and using and managing thousands of plant species (Rostain 2013; Mayle and Iriarte 2014; Clement et al. 2015; Erickson and Balée 2006). The recent progress made by archaeologists and ecologists in documenting human influences on vegetation, both past and present, points to a scenario whereby, after at least 13,000 years of co-evolution between humans, plants, animals, climate, and landscapes, Pleistocene vegetation communities disappeared, and pristine environments became increasingly rare (Erickson 2006; Roosevelt 2014; Balée 2013). Studies show that at least 155 plant species native to the Amazon, Mesoamerica, northern South America, and northeastern Brazil; mostly trees and other perennial species; were domesticated to some degree by pre-Columbian people (Clement 1999; Levis et al. 2017; Box 8.2). These species occur with greater frequency closer to archaeological sites (Junqueira et al. 2010; Levis et al. 2017; Franco- Moraes et al. 2019), and twenty of them are considered hyperdominant (i.e., overrepresented in Amazonian tree communities) (ter Steege et al. 2013), raising questions as to the influence of cultural processes in their distribution (Figure 8.3). Around 200 additional tree species are also deliberately cultivated, and even more are managed, in forest landscapes (Balée 1989; Peters 2000; Levis et al. 2012, 2018), while more than 2,200 species are used today for different purposes by IPLCs (Coelho 2018).

8.5. The Amazon as the center of the first ceramics in the Americas

Ceramic analyses occupy a special place of research in Amazonian archaeology because they tell us about the technological traditions, social relations, and symbolic universes of the people who made and used them. Ceramics not only play an important role in the processing and consumption of beverages and food, but also act as a means of transmitting ideas through their decorative patterns (Lima et al. 2016).

Ceramic production is a technology that developed independently in several places across the world from the Terminal Pleistocene to the Middle Holocene. In the Americas, the earliest centers of ceramic production are located mainly away from the supposed centers of emergence of hierarchical, socially stratified societies, such as the Central Andes and Mesoamerica. Some of these centers are located in the Amazon, where there were at least four independent inventions of ceramic technology: the lower Amazon, the Atlantic coast, the Upper Madeira Basin and the Zamora-Chinchipe Basin in Ecuador. In the first three areas, early ceramics are associated with the construction of artificial shell and earthen mounds (Figure 8.3).

In the lower Amazon, near the current city of Santarém, excavations at the Taperinha fluvial shell mound yielded the earliest ceramics in the Americas, dating back to c. 7,000 BP (Roosevelt 1995; Roosevelt et al. 1991). On the Atlantic coast, east of the mouth of the Amazon in the extensive area of mangroves covering the shores of Pará and Maranhão states, there are dozens of coastal shell mounds and other sites containing ceramics of the so-called Mina phase, dated to 5,500 years ago (Simões 1981; Roosevelt 1995; Silveira and Schaan 2010; Bandeira 2009; Lopes et al. 2018). In the Middle Guaporé Basin, on the border of Bolivia and Brazil, excavations at the Monte Castelo shell mound produced ceramic vessels dating to ca. 5,200 years ago (Pugliese et al. 2017). Finally, in the Zamora-Chinchipe area of the *ceja de selva* of Ecuador, ceramics dated to about 4,500 years ago have remarkable similarities to the later styles of Chorrera and Cupinisque of the Pacific Coast (Valdez 2013), the latter being associated with the emergence of early stratified societies in the Andes.

Away from the Amazon, the other centers of independent early ceramic production in South America are all found in lowland tropical environments, such as Santa Elena province in Coastal Ecuador, the lower Magdalena Basin near Barranquilla, and the Guiana coast (Roosevelt 1995; Oyuela-Caycedo 1995; Raymond and Oyuela-Caycedo 1994; but see Meggers [1997] for a different perspective). Such evidence should be strong enough to refute the hypothesis – more political than scientific – that the tropics are of marginal importance in the early cultural history of South America.

8.6. The formation of anthropic soils (*terras pretas*) and evidence of widespread human niche construction in the middle/late Holocene

Anthropogenic Dark Earther (ADEs) are black to brown, organic-rich anthrosols covering areas up to 90 ha that are found in many archaeological sites in the Amazon dating from ca. 2,500 years BP onwards (Heckenberger et al. 1999; Kern et al. 2004; Neves et al. 2004; McMichael et al. 2014; Clement et al. 2015) (Figure 8.4). These are stable, fertile soils with higher pH and nutrient content (P, N, Ca, Mg) than adjacent soils, conditions that are maintained even under the intense lixiviation of the Amazon (Lehmann et al. 2003, Teixeira et al. 2009). These properties render ADEs valuable for cultivation by modern communities (Clement et al. 2003; Junqueira et al. 2010).

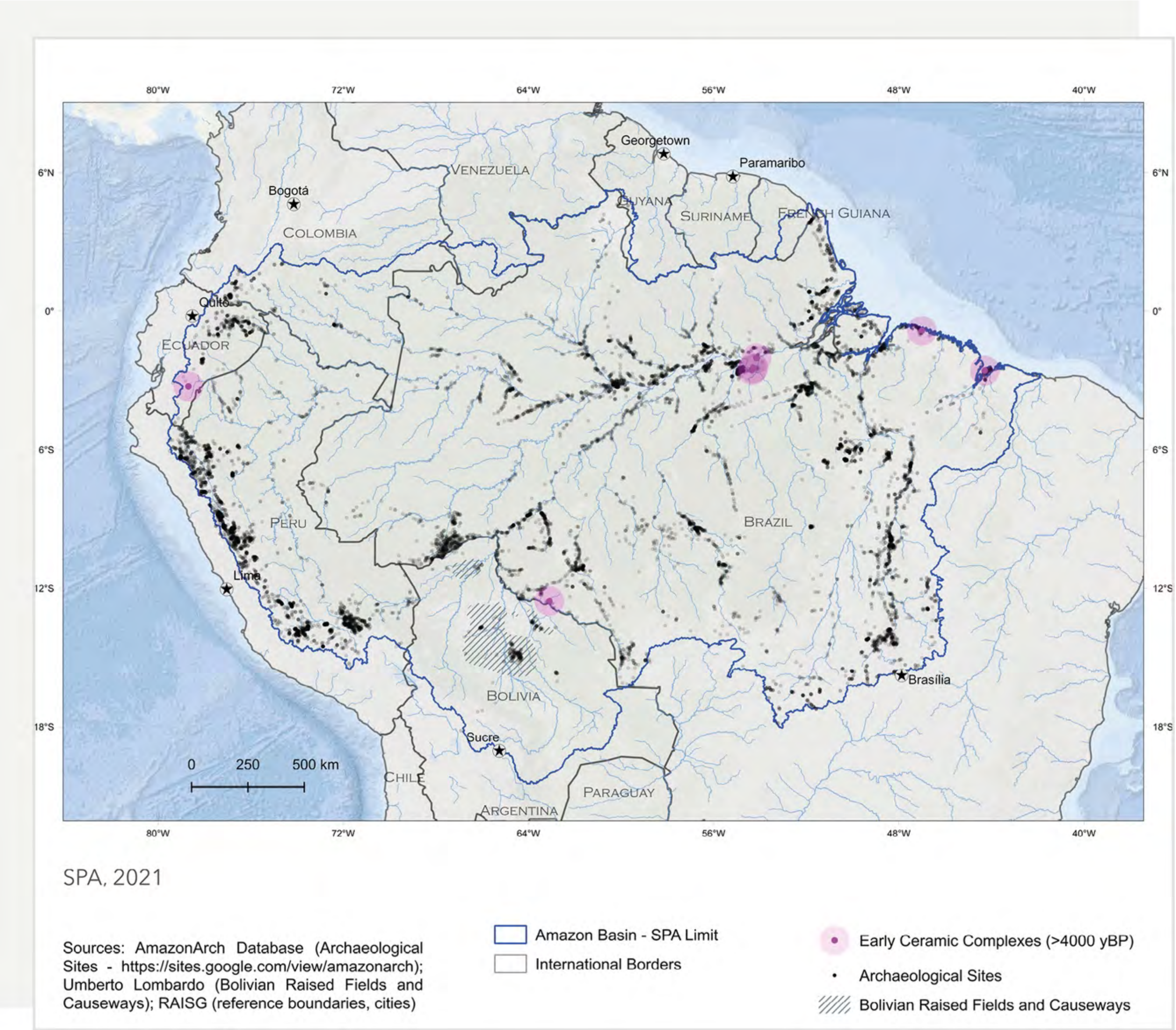
Despite being known to scientists since the nineteenth century, it was only much later that the Indigenous origin of these soils was established (Sombroek 1966; Smith 1980). Today, it is accepted that ADEs are among the most visible and widespread testimonies of past Indigenous settle ments in the Amazon, despite recent claims of their natural origin (Silva et al. 2021) (Figure 8.5). The establishment of the Indigenous origin of ADEs marked a major turning point in Amazonian archaeology, as they attest to past landscape transformations at scales that were previously thought impossible (Petersen et al. 2001; Woods et al. 2009; Glaser and Birk 2012).

Although widespread after 2,500 years BP, ADEs began to form around 5,500 years ago in areas such as the Upper Madeira river in Brazil (Watling et al. 2018) and the Middle Caquetá area in Colombia (Morcote-Ríos et al. 2017), mirroring the pattern of the periphery of the Amazon as centers of plant domestication.

It is possible to distinguish two broad types of ADEs (Sombroek 1966); (i) deeper, blacker soils, often full of artefacts and settlement debris, and very enriched in nutrients, and (ii) shallower, brown, less enriched (but still modified) soils, devoid of artefacts. Studies show that these represent two ends of a continuum of soil modification (which accompanies a continuum of agrobiodiversity Junqueira et al. 2016a, 2016b; Lins et al. 2015), with blacker soils likely having formed as a product of waste management and domestic activities in the core of settlement areas, and browner soils likely the result of cultivation (slash and burn, organic mulching) associated with garden areas on the periphery (Arroyo-Kalin et al. 2012; Schmidt et al. 2014; Alves 2017).

The extent to which ADEs were intentionally created in pre-Columbian times is still debated (Arroyo-Kalin 2016). There is still no agreement on whether they were produced to improve unfertile Amazonian upland soils or if they resulted from the passive accumulation of organic matter from sedentary settlements. The presence of ADEs on the floodplains of the Amazon River near Manaus (Macedo et al. 2017) tends to negate the first hypothesis, since ADEs here developed on alluvial soils that have naturally elevated contents of P, Ca, Zn, Cu that are above agronomic critical levels (Havlin et al. 2005). However, it is also likely that, once formed in upland areas, these soils created new niches that allowed for the cultivation of nutrient-demanding plants such as maize (Rebellato et al. 2009; Arroyo-Kalin 2010).

A study in Santarém combining on-site archaeobotany and off-site paleoecology shows the appearance of ADEs ca. 2,000 BP was accompanied by sys-



Sources: AmazonArch Database (Archaeological Sites - https://sites.google.com/view/amazonarch); Umberto Lombardo (Bolivian Raised Fields and Causeways); RAISG (reference boundaries, cities)

Figure 8.3 Archaeological sites with early ceramics in the Amazon (source AmazonArch)

temic changes in regional plant communities that included increases in edible species (Maezumi et al. 2018). Phytoliths from Bactris/Astrocaryum palms are particularly prevalent in ADE soils located along the Amazon and Madeira Rivers, including at Teotônio, where successive occupations of different ceramic-producing cultures have begun to yield evidence of diachronic variation in plant consumption and cultivation practices through time (Watling et al. 2020b).

8.7. Monumentality and cultural diversity in the pre-Columbian Amazon

In the Amazon, variability of material culture and settlement patterns may be said to match that of Indigenous languages (Neves 2011), although this is not a universal correlation. Since the beginning of systematic research in the region, ceramics have played a key role in mapping the distribution of archaeological cultures or units, largely as a conse-

Sources: AmazonArch Database (Archaeological Sites - https://sites.google.com/view/amazonarch); Umberto Lombardo (Bolivian Raised Fields and Causeways); RAISG (reference boundaries, cities)

Figure 8.4 Archaeological Sites with ADEs in the Amazon (source AmazonArch).

quence of the great quantities in which they are found compared to other cultural remains. Beautifully decorated ceramics from the lower Amazon region quickly caught the attention of 19th century naturalists, gaining ample space in the museum exhibits of different European countries at the time (Neves 1999/ 2000).

The ubiquity of pottery contrasts with a diminished presence of stone artifacts, including lithic tools and rock art (Neves 2006), as well as a near absence of structures built from stone. This pattern probably reflects the irregular availability of stone throughout the Amazon, as well as the universal use of perishable materials such as wood and palm for house building (Novaes 1983), which decompose and disappear with the passage of time, obscuring the dimensions of Indigenous settlements (but see Stampanoni 2016 for the excavation of an ancient longhouse near the Urubu River, in the Central Amazon). The tropical climate and accompanying acidic soils may also frequently erase human and faunal bone remains from the archaeological record (Rapp Py-Daniel 2010), although such remains preserve much better in ADEs due to the almost neutral pH of these soils. The megalithic structures of Amapá present an exception to this. There, large stone slabs were erected on top of underground chambers filled with Aristé burial urns, presenting an example of the convergence of monumentality and mortuary practices (Saldanha and Cabral 2017). The practice of producing mortuary effigies is maintained by some Indigenous groups today, such as the wooden representations found in Kuarup rituals in the Upper Xingu (Guerreiro 2011).

Aside from shellmounds, the earliest evidence of monumentality in the Amazon comes from sites such as Santa Ana La Florida and Montegrande, located on the current border of Ecuador and Peru, along the Upper Marañon Basin (Olivera Nuñez 2016; Valdez 2013). There one finds spiral stone structures, the earliest known evidence for cacao domestication (Zarrillo et al. 2018), exotic goods such as Strombus shells from the Pacific coast across the Andes (Valdez 2013), the earliest evidence of stirrup spout vessels (Valdez 2013), and polychrome murals (Olivera Nuñez 2016). These elements become common in later history but seem to have some of their earlier manifestations in these contexts (Figure 8.6).

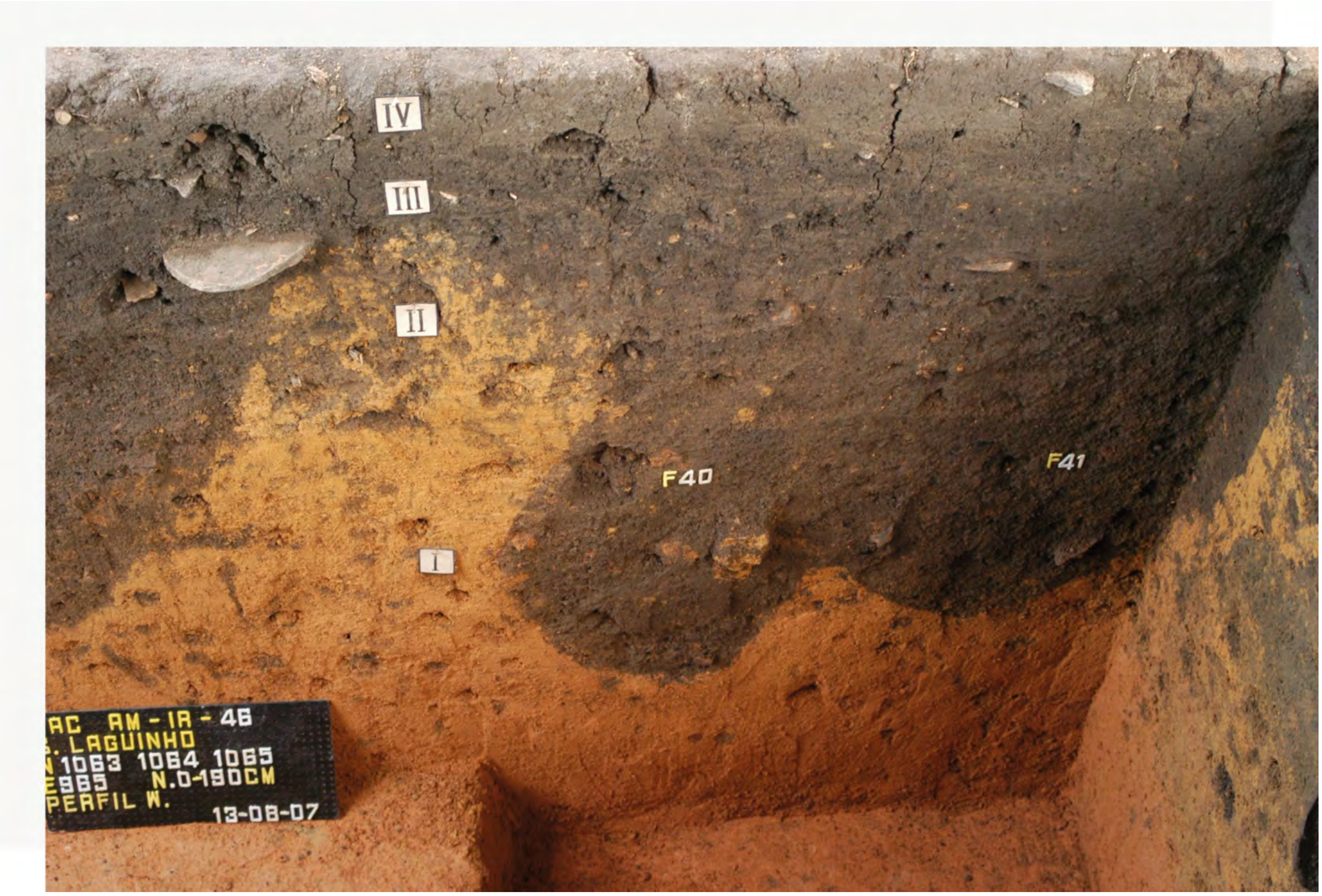
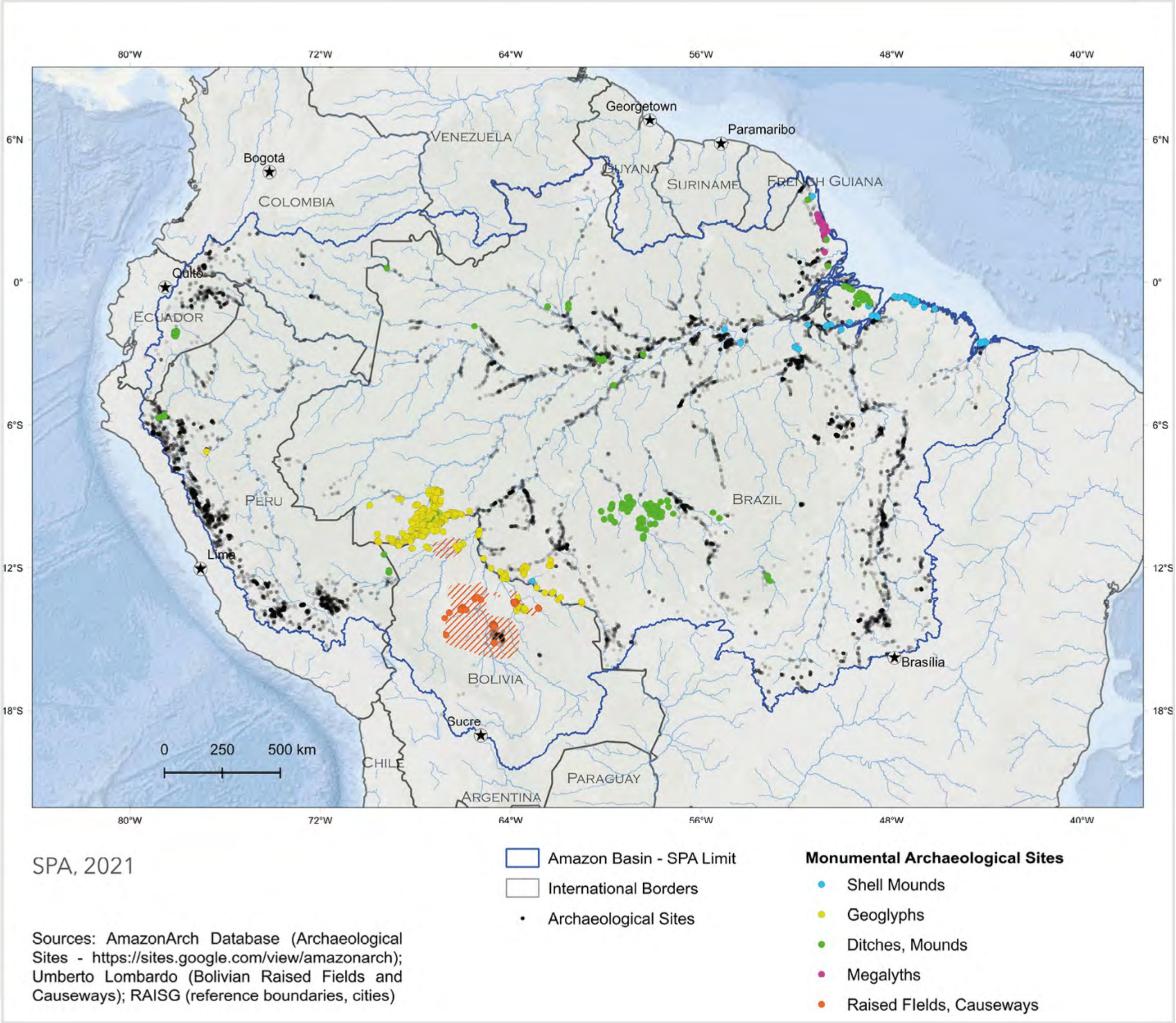


Figure 8.5 Profile cut of ADE soil formed by pits cut into natural yellowish oxisols, Paredão phase (1,300 – 900 BP), Laguinho site, Central Amazon (Photo: Eduardo Neves).

While ceramic vessels date to 7,000 BP, they become more common around 3,000 BP onwards, when archaeological complexes, such as the Pocó and Amazonian Barrancoid traditions, can be linked to the expansion of populations speaking Arawakan languages (Lathrap 1970; Heckenberger 2002; Neves et al. 2014). Around this time, a second wave of earthworks – following the shell mounds – began to flourish. In the Brazilian state of Acre, and neighboring departments of Pando, in Bolivia, and Madre de Dios, in Peru, over 500 archaeological sites consisting of ditched geometric earthworks, including circular and square ditches (up to 7 m deep), have been documented, dating to between 3,000 BP and 800 BP (Ranzi et al. 2007; Schaan 2012; Saunaluoma 2012) (Figure 8.7). Their positions on the tops and edges of natural plateaus (Schann 2012) suggests they were built in locales that commanded good control of their surroundings, while the relative low frequency of artifacts inside them (and the presence of carefully deposited ceramics close to the entrances of the earth-



Sources: AmazonArch Database (Archaeological Sites - https://sites.google.com/view/amazonarch); Umberto Lombardo (Bolivian Raised Fields and Causeways); RAISG (reference boundaries, cities)

Figure 8.6 Areas in the Amazon known to have monumental archaeological sites (source AmazonArch) works) has been argued to indicate they were regional ceremonial centers, rather than settlement sites (Saunaluoma et al. 2018: 363-364).

The same general area was later occupied from ca. 1,000 to 400 BP by people who settled in villages composed of mounds displaced around central plazas and connected to each other by road networks (Iriarte et al. 2020; Saunaluoma et al. 2021). Around the same time, further east in the Brazilian Amazon, a similar pattern of roads connecting much larger settlements was also identified (Heckenberger et al. 2008).

Moving northwest, towards the Ecuadorian Amazon, the concentration of hundreds of platforms, arranged in the form of panels and connected by road systems, is the best example of pre-Hispanic urbanism in the Amazon. According to current data they were built between 2,700 and 1,500 BP (Rostain 1999, 2012; Rostain and Pazmiño 2013; Salazar 2008). LiDAR surveys identified and urban center called Kunguints, composed of hundreds of mounds covering an area of approximately 4.5 km^2, and two wide roads running from the city from west to east (Prümers 2017).

During the first centuries AD, the Amazon experienced a blossoming of cultural styles and an increased flow and mixture of technological traits and exotic materials, suggesting highly connected societies (Heckenberger 2008). Trade materials were manifold, such as the exotic stone ornaments known as *muiraquitãs* (Amaral 2018), ceramics (Van den Bel 2010), and plants. Such specialized trading systems can still be found in regional Indigenous social systems found in the Upper Rio Negro (Neves 2006; Ribeiro 1995) and the Upper Xingu (Franchetto and Heckenberger 2001).

As well as the diversity of ceramic styles, the quantity and variety of earthworks also increased throughout the beginning of the common era. For example, the Iténez region of Bolivia contains a range of features attesting to complex networks of social interaction, including causeway-canal systems (Erickson 2009), fish-traps (McKey et al. 2016), and circular ditched enclosures (Prümers and Jaimes Betancourt 2014). According to LiDAR survey (Prümers 2014), all 24 ditch systems are located on slight elevations, where intermittent streams occur. The largest site was about 200 ha in size and most of the ditches were probably built between 800 to 600 BP.

Intensive surveys in the neighboring Beni Department, Bolivia, also revealed the existence of hundreds of settlement mounds up to 20 m tall and ca. 40 ha in area, generally situated on fluvial deposits of inactive rivers and occupied between 1,500 to 1,600 BP (Lombardo and Prümers 2010). Some of the sites have polygonal embankments that perhaps served a protective function. Canals and causeways connect the sites, and ponds were built, probably to ensure the water supply during the dry season, but also possibly for fish capture (Prestes-Carneiro et al. 2020).

The west-central area of the Llanos de Mojos, west of the Mamoré River, contains the largest, densest, and most diverse concentration of agricultural landscapes in the Amazon (Erickson 2006, 2008; Erickson and Walker 2009). Along the Iruyáñez River there are platforms between 5 and 20 meters wide, 300 meters long, and 0.5 to 1.0 meters high (Denevan 1966, 2001; Erickson 2006; Lombardo 2010; Walker 2004, 2011) (Figure 8.8). Raised-field construction in this area began around 2,500 years BP (Walker 2018). It is possible that the raised fields constituted a complement to other forms of agriculture, since most of them are located on infertile soils and, in the cases where relevant data are available, these point to the fact that they were in use for a short period, followed by a longer fallow time (Rodrigues 2016).

It was also during this period (1,600 to 700 BP) that the Marajoara culture flourished in the savannas of the eastern part of Marajó island (Schaan 2012: 31, Figure 8.9A). These groups constructed mounds on the banks of rivers and lakes, sometimes in groups of up to forty, that they packed with exuberant funerary urns. Some scholars believe that the Marajoara culture was formed by several connected chiefdom societies, who exerted political influence through the construction and control of hydraulic structures such as weirs and artificial fish ponds (Schaan 2010). Marajoara culture is known for pots, figurines, and mortuary paraphernalia with formidable iconography (Barreto 2016). East of Marajó, at the very edge of the Amazonian biome, large villages composed of stilt houses built on seasonal lakes around 1,100 AD and containing materials evidencing long-term trade networks with the mouth of the Amazon are currently being studied (Navarro 2018).

From 1,200 to 400 BP in the Central and Western Amazon, from the Manaus area all the way to the Ucayali, Napo, Içá-Putumayo, and Japurá-Caquetá Rivers, as well as upstream of the Madeira River, one sees sites covered by ceramics belonging to the so-called Amazonian Polychrome Tradition (TPA) (Figure 8.9B). These ceramics, as the name implies, are characterized by painted decoration in distinct tones of red, yellow, orange, or black on a white base. Despite the general similarities, there is considerable variability between ceramics and archaeological sites associated with TPA. The chronology and geographical distribution of these sites show a clear pattern: older in the Central Amazon, younger in the Upper Amazon.

From around 1,000 years BP onwards, in the area around the city of Santarém, Brazil, another ceramic tradition emerged known as Incised-Punctuated, of which the best-known are probably the Tapajonic or Santarém ceramics. These vessels have modeled decoration with anthropomorphic and zoomorphic motifs, such as birds, bats, rep-

Figure 8.7 Geometric square geoglyphs connected by road in area previously covered by forest and currently covered by pasture in Eastern Acre state, Brazilian Amazon, 2,500-500 BP (Photo: Maurício de Paiva).

Figure 8.8 Agricultural raised fields in the flooded savannas of the Iruyañez River, Beni River drainage, Llanos de Mojos, Beni Department, Bolívia (Photo: Heiko Prümmers).

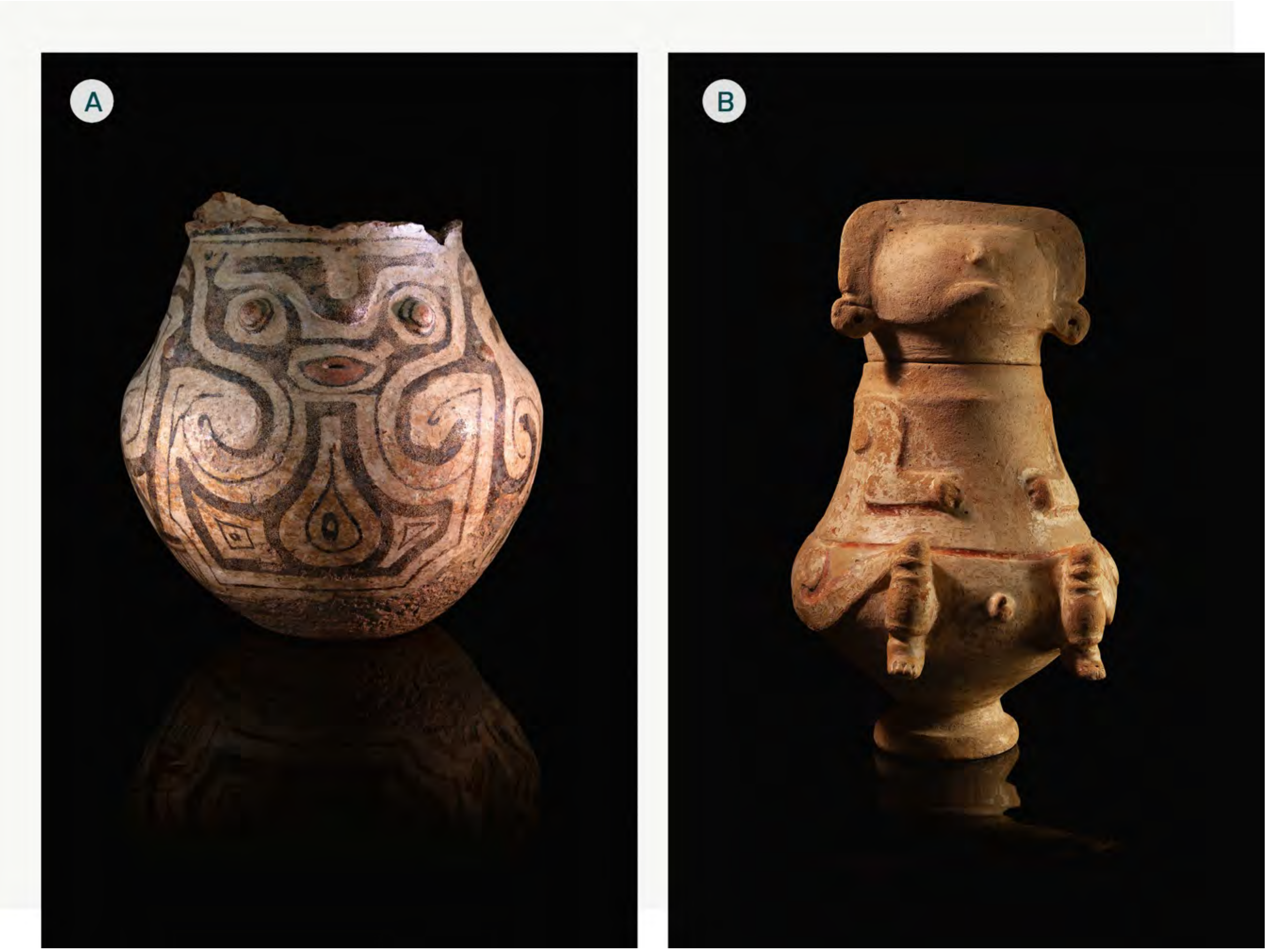


Figure 8.9 A) Polychrome funerary urn, Marajoara phase, Marajó island, mouth of the Amazon, Brazil, 1,600-700 BP, Museum of Archaeology and Ethnology, University of São Paulo (Photo: Maurício de Paiva); B) Anthropomorph funerary urn, Guarita phase, Central Amazon, Brazil, 1,100-500 BP, Museum of Archaeology and Ethnology, University of São Paulo (Photo: Maurício de Paiva).

tiles, and mammals. In Tapajonic ceramics, the presence of naturalistic anthropomorphic statuettes is also common, where details such as body paint, jewelry, and different hairstyles can be perceived (Gomes 2011; Figure 8.10). Tapajonic ceramics are found in a large area whose center is the current city of Santarém, in a large archaeological site mostly destroyed due to urban growth. The few available dates indicate that the Tapajonic occupation began at least at the begin-ning of the second millennium AD, making Santarém probably the longest continuously occupied place in the Brazilian Amazon.

Besides riverine connections, there also existed in precolonial times networks of roads and pathways that connected vast areas of the interfluves (Schmidt 2012; Figueiredo 2018; Saunaluoma et al. 2020, Iriarte et al. 2020; Erickson 2010; Heckenberger et al. 2008), that would later be documented by the first European chroniclers (Porro 1994; Pessoa et al. 2020). The nodes bonding these systems were settlements occupying strategic positions, such as rapids and river junctions. In places like these, large archaeological sites are found and it is common that they are covered by contemporary Amazonian cities such

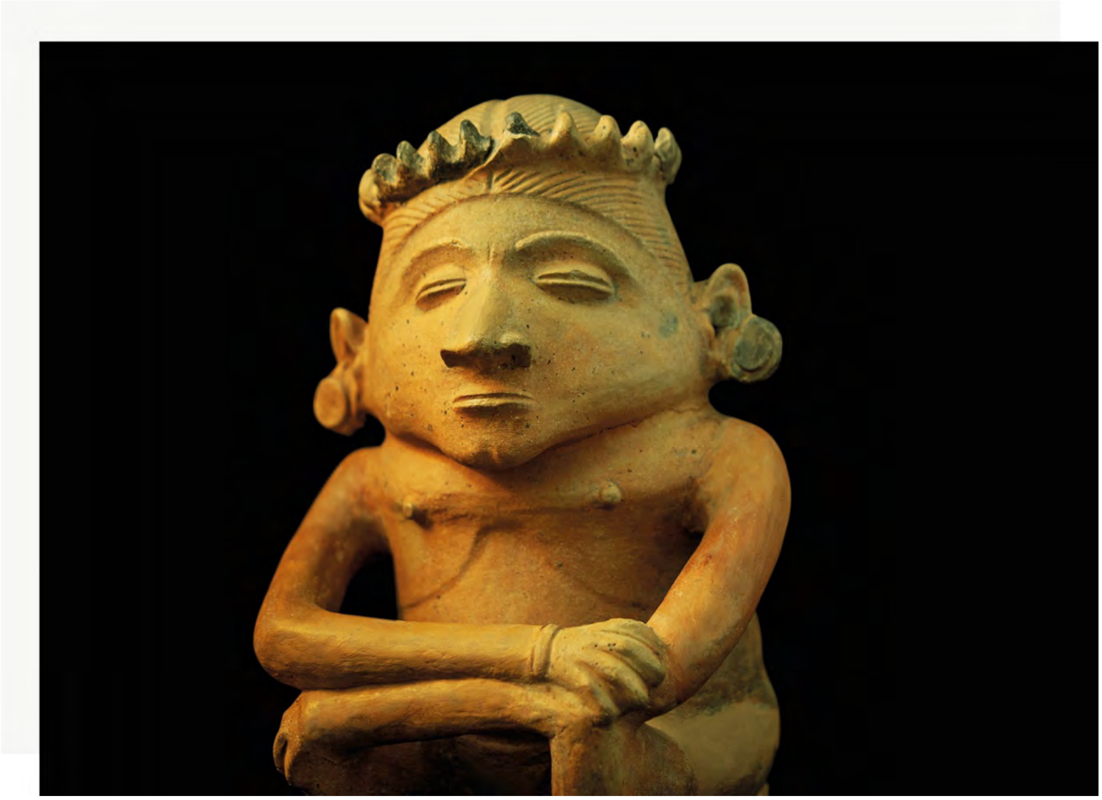


Figure 8.10 Anthropomorph statuette of male figure adorned with earring and tiara sitting on stool, Santarém, lower Amazon, 800-500 BP, Museum of Archaeology and Ethnology, University of São Paulo (Photo: Maurício de Paiva).

Figure 8.11 Archaeologist Márjorie Lima excavating a cemetery of funerary urns at Tauary village, Tefé Lake, Central Amazon, Brazil (Photo: Instituto de Desenvolvimento Sustentável Mamirauá).

as Manaus and Santarém (Almeida 2017). Likewise, archaeological objects commonly make their way into the life of present-day communities, urban and rural, who keep and re-signify them (Bezerra 2013).

In spite of the demographic collapse that took place across the region following the onset of European conquest and colonization, we can state that, over the past 12,000 years, the Amazon has never been an empty space, devoid of people, but has been shaped by an archive of human action. Today, Indigenous peoples and local communities are distributed across areas that were likely more densely occupied and intensively transformed in the past, close to rivers and terrestrial and aquatic resources, leading them to interact closely with the legacies of previous occupation (Figure 8.11). Patches of ADEs are currently inhabited and/or managed by traditional peoples, who have developed detailed knowledge and practices related to their cultivation and management (e.g., Fraser et al. 2012; Junqueira et al. 2010, 2016a, b; Lins et al. 2015). As a result, current forests and food production systems based on ADEs and other archaeological sites are diverse and show singular plant diversity patterns (Lins et al. 2015; Odonne et al. 2019; Levis et al. 2020; Junqueira et al. 2016a, b; Watling et al. 2020a), stemming not only from past modifications of soils and associated plants, but also from their constant transformation through current management practices (Levis et al. 2020; Junqueira et al. 2016b).

The distribution of plant species in the Amazon has been influenced by long-term human actions, particularly species that were once managed, cultivated, or domesticated by Indigenous peoples (Balée 1989, 2013; Clement et al. 2015; Levis et al. 2017). IPLCs recognize the actions of their ancestors in the landscape and often enter into cyclical relationships with local ecosystems by transforming old-growth forests that were once cultivated into swiddens or settlements (Politis 2007; Franco-Moraes et al. 2019). Traditional peoples also play an important role in maintaining past ecosystem legacies through their traditional resource mana-gement practices (Junqueira et al. 2016a; Levis et al. 2020). Domesticated landscapes and plants form an essential element of current livelihoods (Figure 8.12).

For example, at Amanã Lake, a tributary of the lower Japurá/Caquetá River, human settlement c. 3,000 BP generated orchards, gardens, and ADE patches through to the early colonial period (Neves et al 2014). Following demand in the postwar period, rubber-tapper communities moved to the lake and began managing these anthropic forests while creating new gardens. Favored by past societies, species such as bacaba, açaí, cacao, and Brazil nut have persisted, but different landraces of cacao, manioc, legumes, and chili pepper began germinating when 20th century communities began using fire as part of slash and burn agriculture. ADEs had acted as "seed banks" preserving these species, which were then able to regrow after burning (Tamanaha et al. 2019).

Landscapes continuously occupied by IPLCs encompass multiple temporalities and time scales. The multiple connections between pre-Columbian and contemporary traditional management practices evidence how plants and landscapes provide us with a thread of continuity that stretches back millennia, irrespective of biological discontinuities between human populations. This leads us to state that in the Amazon, archaeology is alive and pertains to the present as much as to the past.

8.9. The role of archaeological data and perspectives in evaluating and planning for protected areas

Archaeological research can provide useful perspectives in evaluating current land use and supply valuable subsidies in planning for more efficient and just strategies that recognize the fundamental role and rights of IPLCs. Here, we approach what we consider to be some of the most problematic issues related to the creation and management of current protected areas, including Indigenous lands, traditional peoples’ territories, and conservation units.

All categories of protected areas overlay IPLCs' territories. These territories are socially and historically constituted, and encompass different landscapes in which many land uses, including habitation, resource extraction, gathering, cultivating, fishing, hunting, fallows, and sacred or meaningful places, are present (e.g., Posey 1985). The recognition of the multiple uses of territory is too often ignored by policy makers and governments, who consequently exclude areas important to IPLCs, disenfranchising them from their territories. The boundaries of traditionally occupied territories can also be thought of as meeting places rather than barriers (Gallois 2005), at times overlapping with those of other social groups; such interactions can be observed in ancient material culture as well as through linguistic borrowing (e.g., Rocha 2020b; Rodrigues 1985). The overlap of territories from different communities is not usually considered in the definition of protected areas, generating conflicts among neighbors.

Conservation units (CUs) tend to be defined by criteria related to "nature," often ignoring social dimensions. CUs fall within two basic categories, strict-protection Nature Reserves in which human occupation is prohibited, and Sustainable Use Conservation Units where people live so long as they abide by regulations. In the Brazilian Amazon, there is a systematic pattern of imposing strict-protection Nature Reserves on territory traditionally occupied by IPLCs (Almeida 2004; Almeida et al. 2018; Balée et al. 2020; Coelho et al. 2017; O’Dwyer 2002; Torres and Figueiredo 2005; IBDF 1984). This has been justified through the supposed existence of ‘empty’ lands and ‘pristine’ forests; however, as we have demonstrated, the co-occurrence of well-preserved areas and traditional Amazonian peoples is no coincidence. Imposed restrictions have had the effect of outlawing traditional practices inextricably linked to traditional peoples' dietary habits and ways of life. These, as we have seen, can in fact be congruent with the aims of conservation and contribute to the promotion of biodiversity, ecosystem services, and food security (e.g., Balée et al. 2020; Levis et al. 2018; Scoles and Gribel 2015; Torres 2011). Gradual and direct expropriation of communities as a result of these policies has exposed these areas to predatory invasion. CUs that allow for the presence of traditional peoples have been shown to be more coherent with the already recognized millennial human use of biodiversity – so long as they are not conceded to private enterprise in top-down initiatives, in contravention to ILO C169 (Nepomuceno et al. 2019).

At present, only a fraction of traditionally occupied territories have been officially recognized. With regard to *quilombola* communities in the Brazilian Amazon, this only amounts to ~899,000 hectares, representing 0.26% of all *quilombola* territories (Levis et al. 2020). Other peoples' traditionally occupied territories, often invisible to the eyes of the State, are in a similar situation. Land insecurity exposes IPLCs to the advance of predatory activities, imposed through violence and intimidation, which often become the only viable alternatives for them to sustain themselves. Archaeology further helps us understand that IPLCs transmitted knowledge orally across generations about their histories and territories. These memories are often anchored in specific landscape markers, highlighting how in the Amazon ecocide and epistemicide are two sides of the same coin.

8.10. Indigenous peoples and local communities’ archaeologies

From its inception as a discipline, archaeology was employed as a powerful element in the construction of ethnic, national, and imperial identities. Until recently, this endeavor was carried out by elite groups, or to suit reigning political interests. Over the past few decades, pressure from other groups, who actively began claiming the past for themselves (Politis and Curtoni 2011:

496) by including archaeological sites (and specific remains) as part of their political discourse (Bezerra 2012, 78), has contributed to changing this scenario, leading the discipline to reconsider its role and responsibilities towards claimants, in particular marginalized IPLCs.

In the Amazon, archaeological research undertaken in close collaboration with Indigenous peoples was inaugurated at the turn of the millennium (e.g., Heckenberger 1996; Silva 2002). The creation of undergraduate archaeology courses at public universities in Brazil such as the Federal University of Western Pará, Federal University of Rondônia, and Amazonas State University, has enabled members of IPLCs to enter the discipline. These scholars have begun appropriating archaeological tools while offering critiques and novel contributions to archaeological concepts, as well as opening up new avenues for research (e.g., Munduruku 2019; Parintintin 2019; Silva 2018; Wai Wai 2019; Wai Wai 2017). Among these concepts, of utmost importance is that of sacred place. Sacred places can be present within potent features in the landscape; they may include archaeological remains such as rock art or concentrations of medicinal plants, or be "invisible" in archaeological terms. Access can be regulated according to specific norms and may be restricted except to the initiated. They are often salient topographical features and may house supernatural entities, such as spirit mothers of fish or game animals, or they may be where significant mythical-historical events occurred (Rocha 2020a). The violation of sacred places is thought to result in grave misfortunes, accidents, and diseases (Baniwa 2018).

Encounters between IPLCs and archaeology have also occurred within wider contexts of conflict and human rights violations spearheaded by the expansion of capitalist frontiers (development of infrastructure such as dam and road building) within environmental licensing frameworks (Bezerra 2015; Rocha et al. 2013) (Figure 8.13). The construction of dams on the Teles Pires River, a tributary of the Tapajós in the southern Brazilian Amazon, led to the destruction of important sacred places for the Munduruku, Apiaká, and Kayabi peoples. Here the “salvaging” of funerary urns by archaeologists was considered by the Munduruku as a violation of ancient cemeteries (Pugliese and Valle 2015, 2016). This has resulted in perhaps the first instance of an archaeological heritage-related direct action in Brazil, as on Christmas day 2019 the Munduruku occupied the Alta Floresta Natural History Museum, performed rituals, and reburied the funerary urns. This suggests that archaeologists must follow consultation protocols in line with the International Labour Organization’s Indigenous and Tribal People’s Convention (ILO C169), which guarantees the right to free, prior, and informed consent in relation to actions and projects that will impact their territories and heritage.

8.11. In the Amazon, natural heritage is cultural heritage: Recommendations for policy makers

The study of technological developments, material culture, language dispersals, monumental constructions, and networks linking peoples in disparate locations should put to rest the idea of the Amazon as a “pristine” peripheral region with nothing else to offer other than hydropower energy, mineral resources, and timber; as an exit corridor for commodities; or a repository of state-owned lands to eventually be turned into pasture or soybean plantations. This model has clearly failed and is putting Amazonian peoples and ecosystems – as well as the rest of humanity – at risk. Amazonian archaeology shows that we have much to learn from Amazonian peoples past and present and provides a means to help do historic justice to the region as a center of history, knowledge, and culture in its own right.

By unearthing the role played by ancient Amazonians in configuring forest and urban landscapes, and by studying relationships between agrobiodiversity, landscape legacies, and the region’s current plural societies, archaeology can provide a long-term perspective and concrete examples of pathways leading to the preservation and restoration of the region.

8.12. Conclusions

The archaeological heritage of the Amazon, which, as we have seen, includes its natural components, is now being destroyed at a faster pace than ever before. From the perspective of archaeology, any solution conceived for the Amazon must necessarily have at its center Indigenous peoples and local communities, whose very identities are closely linked to their traditionally occupied territories (Almeida 2004), of which they are guardians. They know best how to make good use of them. Guaranteeing collective land rights for IPLCs is the most effective way of conserving biodiversity in the Amazon and worldwide (Walker et al. 2020; Garnett et al. 2018).

8.13. Recommendations

- IPLCs' territorial rights must urgently be recognized and guaranteed. Not doing so exposes them and their territories to violence, invasion, degradation, and disease, and can accelerate forest degradation and biodiversity loss. Furthermore, their rights to self-determination must be upheld.
- Strict-protection nature reserves whose interiors have been traditionally occupied should be reconfigured to allow traditional peoples to remain and continue their ways of life, preserving their natural-cultural heritage.
- The fact that different traditional and/or Indigenous peoples may have areas of common use within their different territories needs to be contemplated by legislation, since not doing so has generated conflicts between neighboring communities.
- Prior to territorial demarcation, in-depth research about, and inclusion of, the peoples affected and their natural-cultural heritage is a *sine qua non* condition so that the relationships between the affected communities, the land, and their neighbors is adequately taken into account and future conflicts are avoided.
- In configuring protected areas (which include Indigenous lands, conservation units, and traditional peoples' territories), land use beyond habitation zones must be taken into account (e.g., hunting and resource extraction areas and sacred places) and anthropogenic forests must be understood as natural-cultural heritage.
- The inclusion of social scientists as well as IPLCs (in a way that respects their forms of social organization) in the creation and management plans for protected areas is needed to properly contemplate community specificities and territorial use.
- Further initiatives from state agencies and the third sector are needed to support IPLCs to generate incomes from the agrobiodiversity they have created and managed for millennia and to enable them to continue to provide vital ecosystem services.
- The use of controlled, localized, low temperature fires by IPLCs is a historical management strategy, important to their cultivation and forest management practices, that prevents wildfires in dryer periods. We encourage the incorporation of traditional people and their knowledge on fire use in environmental management strategies led by state agencies within protected areas.
- IPLCs' territories concentrate "islands of forests" surrounded by agro-pastoral fields. Because of climate change and deforestation (particularly from invasions) around their territories, abrupt and more flammable forest borders are created. We recommend the creation of protection and buffer zones around these territories, particularly the creation of corridors of protected lands that allow preservation of environments and ensure proper communication between their human and non-human inhabitants.
- Education paradigms within and without the region must shift to incorporate archaeological knowledge of the Amazon, in order to furnish society at large with a more accurate historical conception of the region that takes in the

fundamental contributions of Amazonian peoples to both national and global development.

- Intercultural education and museum projects constructed with IPLCs must be installed in order for local histories and knowledge to serve as a central reference to empower IPLCs, rather than sole focus on historical developments of national societies that are far-removed from local realities.
- Funding for local archaeological and other interdisciplinary research, which includes and is designed by IPLCs and geared towards their needs, must be encouraged, allowing for the co-production of knowledge.
- Pre-Columbian Indigenous societies developed technologies with long-lasting impacts that were highly adapted to Amazonian conditions – such as ADEs, raised-fields, and agroforests, which optimized development and the expansion of food production systems. These technologies can inspire new forms of urbanism, waste management, and land-use systems highly integrated with the Amazon’s natural conditions, with the potential to boost sustainable solutions for the Amazon.
- Decisions on infrastructure and other development projects should be taken with consideration to ILO C169. This involves collaborative assessments of impacts to IPLCs' heritage. Environmental licensing should therefore enable such decisions on technical, rather than political, grounds (Fearnside 2015), rather than serving as a "bureaucratic ritual of territorial occupation" (Folhes 2016).
- The countries of the Amazon Basin will have to seek the means to adopt variables of these measures in a community way, thus favoring not only the protection of many Indigenous peoples but also the conservation of Amazonian biodiversity.

These recommendations support the overall aim of consolidating IPLCs' autonomy, so that they are able to decide on their collective futures, which necessarily involve the Amazon's stability and integrity.

8.14. References

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Chapter 9

Peoples of the Amazon and European colonization (16th-18th centuries)

Indígenas Kanamari durante trabalho na roça da aldeia Massapê (Foto: Bruno Kelly/Amazônia Real)

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Graphical Abstract

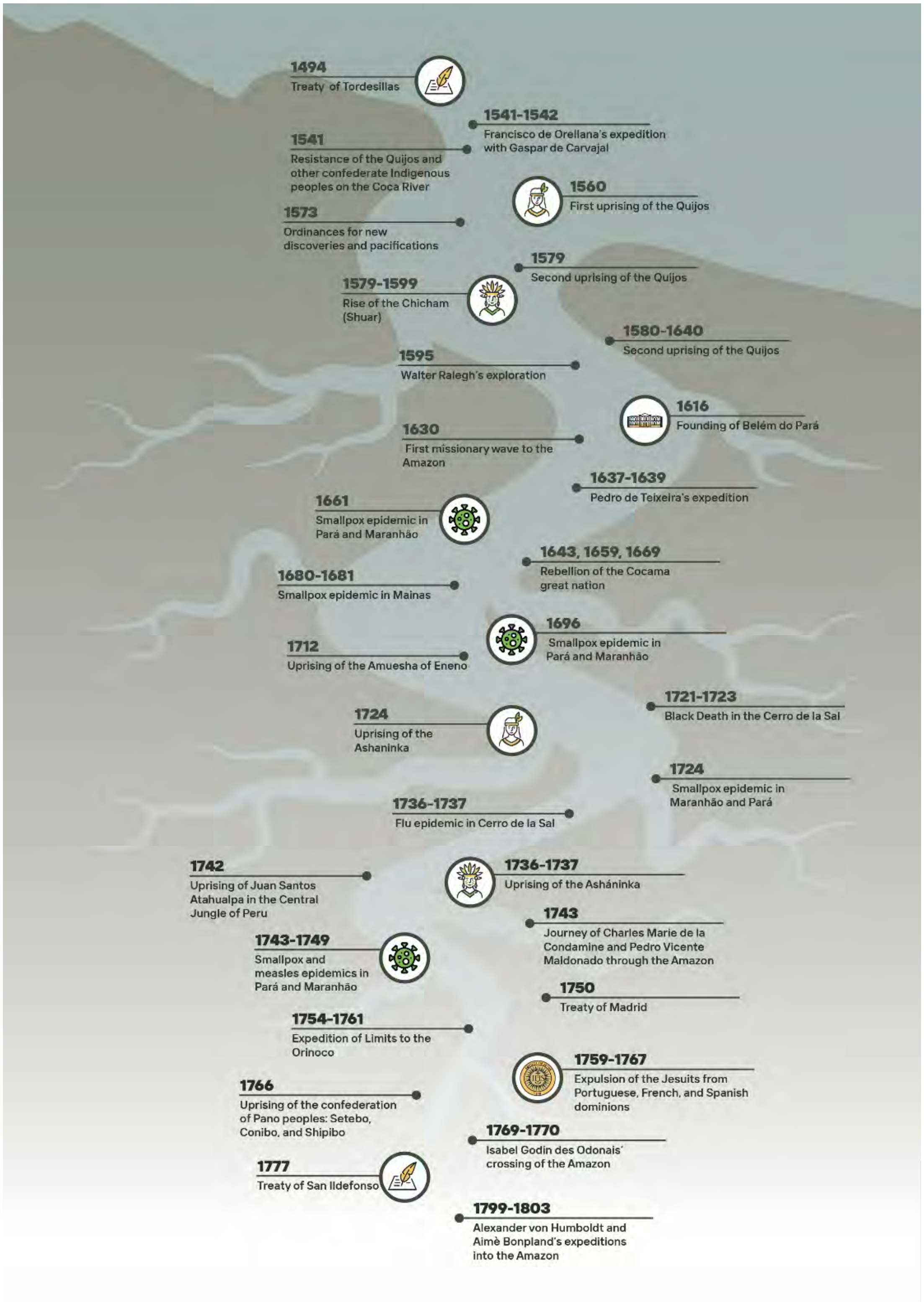

Figure 9.A Graphical Abstract

Peoples of the Amazon and European Colonization (16th - 18th Centuries)

Nicolás Cuvi[a], Anna Guiteras Mombiola[b]*, Zulema Lehm Ardaya[c]**

Key Messages

- The 16th–18th centuries left traces on the Amazon, such as its name. Several myths remain, built around a wealthy (metals, medicines, materials), marginal, distant, dangerous, and sometimes empty (as a result of depopulation) space, attractive for the appropriation and mobilization of knowledges.
- Colonial notions such as those based on the "civilization/barbarism" duality have strongly influenced political and social relations with the political-administrative centers of kingdoms and republics, and between Indigenous and non-Indigenous peoples. For example, there is a constructed opposition between activities considered as signs of "civilization," such as extensive agriculture, in contrast with hunting, fishing, forestry, or subsistence agricultural systems. These kinds of dichotomies often appear in the region's development policies and proposals.
- The construction of "borders", "limits," and "frontiers" was also recurrent in the territory; between the European kingdoms and the inheriting States of the Spanish, Portuguese, Dutch, English, or French colonies; between the mountains and the plain; or among Indigenous peoples. Those borders ignore various dynamics of intense exchange, such as those performed between the Amazonian territories and the coasts and high Andes.
- The relationship between Indigenous peoples and European conquerors and colonizers was usually violent and defined by tensions in which processes of military and religious domination met with resistance. The Amazonian peoples subjected to missions underwent ethnogenesis, which gave rise to new identities containing both traditional and missionary elements.
- Demographic decline contributed to perpetuating the myth of the "great Amazonian emptiness" and the division between the Amazon and the Andes. The extinction of many Indigenous peoples because of contact with non-Indigenous agents and "civilizing" policies draws attention to the continuity of this dynamic through to the present, highlighting the vulnerability of Indigenous peoples in initial contact or voluntary isolation.
- The introduction of technologies such as iron tools created both new relations and tension between Indigenous peoples, and between them and colonists.
- Several cities were located in areas occupied by Indigenous peoples, whereas others were built in new places.

Abstract

This chapter deals with the history of the Amazon between the 16^{th} and 18th centuries. It is organized according to various themes that have left indelible traces on the territory, in some cases up to the present day. The name of the Amazon River and subsequently of the whole region illustrates the influence of European myths. Several legends have been woven about the Amazon since then, including that of harboring

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potential inexhaustible riches or being a dangerous and empty space (largely owing to the depopulation of Indigenous peoples). “Borders” were also established in the Amazon in many ways; between Indigenous peoples, between “civilization” and “barbarism,” between urban and savage, between Catholicism and paganism, between the Andes and the Amazon, and between Brazil, colonized by Portugal, and the Andean-Amazonian countries colonized by Spain.

Key actors in European colonial expansion were military explorers, state officials, missionaries, and scientists. They built a narrative that combined fantasy with truthful information that included ethnographic descriptions as well as maps of the location of waterways, populations, natural resources, and natural history. They were also central to the establishment of urban centers.

Since the era of European conquest, the extraction of natural resources has been accompanied by subjugation and exploitation of the workforce and the development of multiple forms of domination and extermination, especially of Indigenous peoples. Moreover, conquest and colonization of the Amazon implied drastic changes in the relationships within Indigenous societies, between Indigenous peoples, and between these peoples and the agents and representatives of the colonial states, varying significantly between the kingdoms of Spain and Portugal. In turn, Indigenous peoples have accumulated various forms of resistance and rebellion to preserve their ways of life, territories, and autonomy. This chapter contributes to an understanding of the Amazon as a result of the accumulation of multiple and diverse long-standing determinations.

Keywords: Amazon 16th–18th centuries, explorations, cartography, colonial rule, cultural imposition, slavery, myths, epidemics, resistance, religious missions, extermination, urbanization.

9.1 Introduction

Because of the sluggish economy on the Iberian Peninsula, one of the most important incentives for maritime exploration in the 15th century, especially by the Portuguese and Castilians (later Spanish), was the search for alternative routes for trade with the Far East, which had been hampered by the expansion of the Ottomans and the taking of Constantinople. In the late 15th and early 16th centuries, English, French, and Dutch ships joined these explorations. In this economic context, Christopher Columbus set sail from the port of Palos (Spain) in 1492 and, two months later, arrived at Guanahani Island in the Caribbean, unaware that it was another continent.

Additional Spanish expeditions departed from the Caribbean, leading to Spanish expansion through Mesoamerica and South America, following the Atlantic coast to the Orinoco River, and the Pacific coast to the heart of the Inca empire. The Inca empire was experiencing a civil war when Europeans arrived, making it easier for the Castilian Francisco Pizarro and his people to seize power and, therefore, control a good part of the territory. In the process of the fall of the Incas, conflicts among the conquerors erupted, notably one faced by Pizarro and Diego de Almagro, both serving the Spanish monarchy. At the same time, the Portuguese, more interested in preserving their enclaves on the African coast to maintain their trade with Asia, established some ports on the eastern Atlantic coast.

The first explorations of the Amazon were organized from the coastline controlled by the Portuguese, and from the Andes in the hands of the Spanish. Those on the Iberian peninsula were living in a time of transition between the Middle Ages and the modern age, in the midst of the emergence of the Renaissance. In a worsening context of conflict between Christians and Muslims, particularly in the kingdom of Castile, and the revival of the idea of the Crusades, their imagination was shaped by biblical stories, chivalric novels, and Greek mythology. With this economic, cultural, and social baggage, the conquerors explored what they described as a “strange region” inhabited by complex societies (see chapter 8) that they named the “country of the Amazons”, which included places such as the Country of Cinnamon, El Dorado, Gran Paititi, Gran Mojo, and even Eden. The newcomers were guided by three principles: gold, personal glory, and gospel (Velásquez Arango, 2012).

This chapter shows the initial impact of these ideological, economic, social, and cultural clashes, as well as other trends generated during the era of conquest and colonization, many of which have lasted up to the present. Some processes that took place between the 16th and 18th centuries were: expeditions that navigated the great Amazon River and its Basin; ruptures and reconfigurations of the relations between the Andes and the Amazon; expeditions in search of mythical places and knowledges; demographic and cultural impact on Indigenous populations; establishment of cities, missionary settlements, and institutions of colonial rule; Indigenous resistance and rebellion; and, last but not least, the delimitation of boundaries between the Brazilian Amazon and the so-called Andean-Amazonia.

The topics within each section follow a chronological order, covering some decisive events during the entire period of the European conquest and colonization of the Americas.

9.2 Arrival of the Spanish and Portuguese: From Gaspar de Carvajal to Cristobal de Acuña and the origin of the name of the Amazon

The Amazon owes its name to “the Amazons” mentioned in the accounts of Gaspar de Carvajal in 1541–1542. In America, the first chronicles of conquest correspond to a genre that “is part history, part fiction, and part description of geography and nature [...] In this narrative, the chronicler is a witness or participant in the events he describes” (Carrillo 1987: 27). Reading sources from the 16th century requires understanding of the subjectivity of the conquerors. Their stories give an account of the interests and cultural load that they brought from the old continent: the search for valuable spices from the Far East in the Country of Cinnamon, El Dorado, El Paitite, El Enim, or El Gran Mojo, including stories that interpret what they saw based on Greek mythology.

Some attempts to explore the Amazon occurred in the 1530s. One expedition departed from the Atlantic coast, through the Maranhão, led by Aires da Cunha in 1535. The other left in 1538 toward the eastern foothills and reached the river Huallaga, a headwater of the Amazon. The leader, Alonso de Mercadillo, sent 25 horsemen to explore the country. Led by Diogo Nunez, after 25 days they reached a land full of Indigenous peoples with gold ornaments. They fought these people and moved on to the territory of a prosperous, well-organized people called Machifalo or Machiparo, whose many villages lay on the upper Amazon (Hemming 1978: 184-185).

After those first explorations, Francisco Pizarro appointed his brother Gonzalo as Governor of Quito. There, rumors suggested that the Country of Cinnamon or El Dorado were to the east, towards the interior of those lands. Gonzalo decided to organize an expedition, managed to gather 220 Spaniards and 4,000 Indigenous people, and also summoned Francisco de Orellana, who reached him at the intersection of Napo and Aguarico. Having decimated his supplies, they agreed that Orellana, with 57 men and the Dominican Gaspar de Carvajal, chronicler of the expedition, would advance in search of settlements to obtain food for the entire expedition. They were to return in 3 or 4 days after their departure. Either because he wanted to get ahead to claim the lands that were discovered or, as he himself stated in the trial that later followed in Spain, accused by Gonzalo of treason (of which he was exonerated), being unable to return against the current and being worried to face the danger of mutiny from the people who accompanied him, Orellana decided to continue downstream, along the Napo River, until they found a great river through which they continued to navigate for several months until they reached its estuary at the ocean (Carvajal [1541-1542] 2007).

Figure 9.1 Detail of a World map showing the Amazons, 1544. Source: Cabot (c.1544).

Gaspar de Carvajal described that, having been attacked by Indigenous peoples, including some warrior women, they took one prisoner, who gave information about a large town made up exclusively of women who lived in more than 70 villages, led by one called Coroni. The chronicler portrayed them as very white and tall, with long hair, braided and tousled at the head, “very thick and they walk naked in hides covered with their shame, with their bows and arrows in their hands, waging as much war as ten Indians” (Carvajal [1541-1542] 2007: 22). They were referred to as the Amazons. The connection of the term with the great river took a little longer. Even upon their arrival to the Atlantic Ocean, it was called Marañon, and from then on as *Río Orellana*. Only later did it receive the name Amazon (Carvajal [1541-1542] 2007). The “discovery” was of such importance that only two years later, Sebastiano Caboto included the river and the myth of the Amazons in a Planisphere that was published in Venice in 1544 (Figure 9.1).

Almost a century later, between 1637 and 1639, Pedro de Teixeira departed from Pará, arrived in Quito, and made the return route accompanied by the Jesuit Cristóbal de Acuña, who wrote the chronicle of a new discovery of the Amazon River. He ratified Carvajal’s narrative about the warrior women, thus consolidating the name of the great river (Carvajal, Rojas y Acuña 1941:265-266).

The chronicles of Carvajal and Acuña illustrate the diversity of peoples and languages encountered, and the large populations and abundance in which Indigenous Amazonians lived. However, between the Orellana–Carvajal and Teixeira–de Acuña expeditions, the Omagua populations were almost extinct as well as other populations from the estuary of the Amazon River (Carvajal, Rojas y Acuña 1941:111).

Why did this region collect such a large number of myths, more than others in the Americas? (Pizarro 2009: 13-81). Some authors cited in this chapter point out the geographical similarity of the region with biblical stories, Greek writings, and chivalric novels, which referred to Eden, places of gold, great wealth, and strange beings that, with the spread of the printing press, circulated in the Iberian Peninsula with a seal of veracity. However, owing to its permanence in time, one aspect must be highlighted: the Amazon also became a privileged expression of the notion of borders in the sense of the “unknown” and “the other,” of that beyond a “civilized” center, an inexhaustible source of myths (Velásquez Arango 2012).

9.3 Millennial and more recent relations between the Andes and the Amazon

South American mountains and plains have been linked over time in different ways. Increasing evidence supports that their supposed division, associated with geographical, climatic, landscape, and cultural issues, has been a myth (Pearce *et al.,* 2020). Long before the Spanish conquest, Indigenous peoples who inhabited the so-called *piedemonte* or foothills were fundamental in this connection. They were intermediaries between the mountains and the jungle plain, mobilizing knowledges, myths, and hundreds of products through those vast territories.

For the Incas, the Amazon was the *Antisuyu*. Several groups from that region were assimilated by them (sometimes forcefully, sometimes voluntarily), before the arrival of the Spanish. In some places, their influence lasted, and because of this and previous relations, the Spaniards encountered many “Andean Indigenous peoples” in the foothills. However, evidence of this expansion and its precise territorial scope is controversial and continues to provoke debates and research (Moore 2016).

With conquest and subsequent processes of depopulation and resistance, part of that connectivity was lost. Eventually, this apparent disconnection led, among other things, to the idea that lowlands and highlands were clearly separated territories. An imaginary border was built between “civilization” and “savagery” or “barbarism”. Administrative borders of townships and provinces were established up to the so-called eastern borders, although in practice they were highly permeable.

During European colonization products, such as coca, essential in mining operations, flowed widely from east to west. The foothills were never a barrier, but an elastic meeting space of material and symbolic exchange, a transitional place whose meaning was complex and evolving, a place of escape or one of confinement, always a refuge (Saignes 1981; Renard-Casevitz, Saignes and Taylor 1988).

Myths such as the Amazons, Paitite, Enim, or El Dorado contributed to the construction of an unknown and hostile territory beyond the border, but one that was also attractive; Paitite sparked many Spanish expeditions toward the Andean–Amazonian slopes.

Like their Inca predecessors, the conquerors encountered fierce resistance to their expansion in the foothills and plains. According to Saignes (1981:175), "the Spanish failure to settle in the foothills is due both to the lack of large mineral deposits and to the impossibility of exploiting the Indigenous labor force." They also found a different kind of nature, less domesticated and familiar.

An illustration of how relations between the mountains and plains were portrayed appears on a map possibly drawn by the religious Hernando de la Cruz from a sketch by the Portuguese pilot Benito de Acosta, presented by Cristóbal de Acuña in 1640 (Burgos Guevara 2005) (in the catalogue of the National Library of Spain, it is attributed to Martín de Saavedra and Guzmán and dated 1639) (Figure 9.2). In that map, one of the first of the Amazon River, the connection between Andean glaciers and the Atlantic Ocean appears to be articulated by the river. The same is observed in the map of the French academic Charles Marie de la Condamine in 1743, after his scientific trip through the river with the Creole Pedro Vicente Maldonado (Figure 9.3). In both cartographies, the river and plains were drawn in relation to the mountains.

The water determined the main routes for the initial explorations of gold-seeking soldiers, then of missionaries, and finally of adventurers in search of treasures, including minerals and natural products (Chapter 12).

9.4 More explorations of the Amazon

Explorations of the Amazon carried out by Europeans, most of them with the support of Indigenous peoples, combined greed and curiosity. The first centuries of conquest and colonization witnessed raids by explorers dressed as soldiers, missionaries, scientists, or "entrepreneurial" adventurers such as the *bandeirantes*. Their motivations included the control and possession of territories, appropriation of gold and plants such as cinnamon, slavery, and establishment of settlements. Over time, missionary and scientific interests increased around cartography, geography, natural history, and ethnography, sponsored or endorsed by commercial interests. All of these interests remain until this day, for example in mineral and oil prospecting, bioprospecting for useful plants, or research on ecology, biology, hydrography, climate change, and ethnography.

The kingdoms of Spain, Portugal, England, France, and Holland vied for appropriation and control of the territory. In the 16th century, the Spaniards organized expeditions from Quito, the site in the Andes closest to the plain, using traditional routes that facilitated intensive exchanges as between the highlands and lowlands for millenia (Burgos Guevara 2005). The Portuguese, on the other hand, sailed "upstream," whereas the English, French, and Dutch entered mostly from present-day Guiana and Suriname.

Early travelers were fundamental in generating myths that alluded to the dangers and richness of the Amazon. Among the most famous were a city of gold (El Dorado), a Country of Cinnamon, and a territory of warrior women they called Amazons. They also spread the idea of a city or place called Paitite, where the Inca nobility would have taken refuge after the conquest. That place still flows between imagination and reality (Tyuleneva 2003). Sometimes it was confused with the myth of the fabulous empire of the Enim. Myths were fueled by stories such

Figure 9.2 Map of the Amazon, 1640. Source: Saavedra y Guzmán (1639).

Figure 9.3 Map of the Amazon, 1745. Source: Condamine (1745).

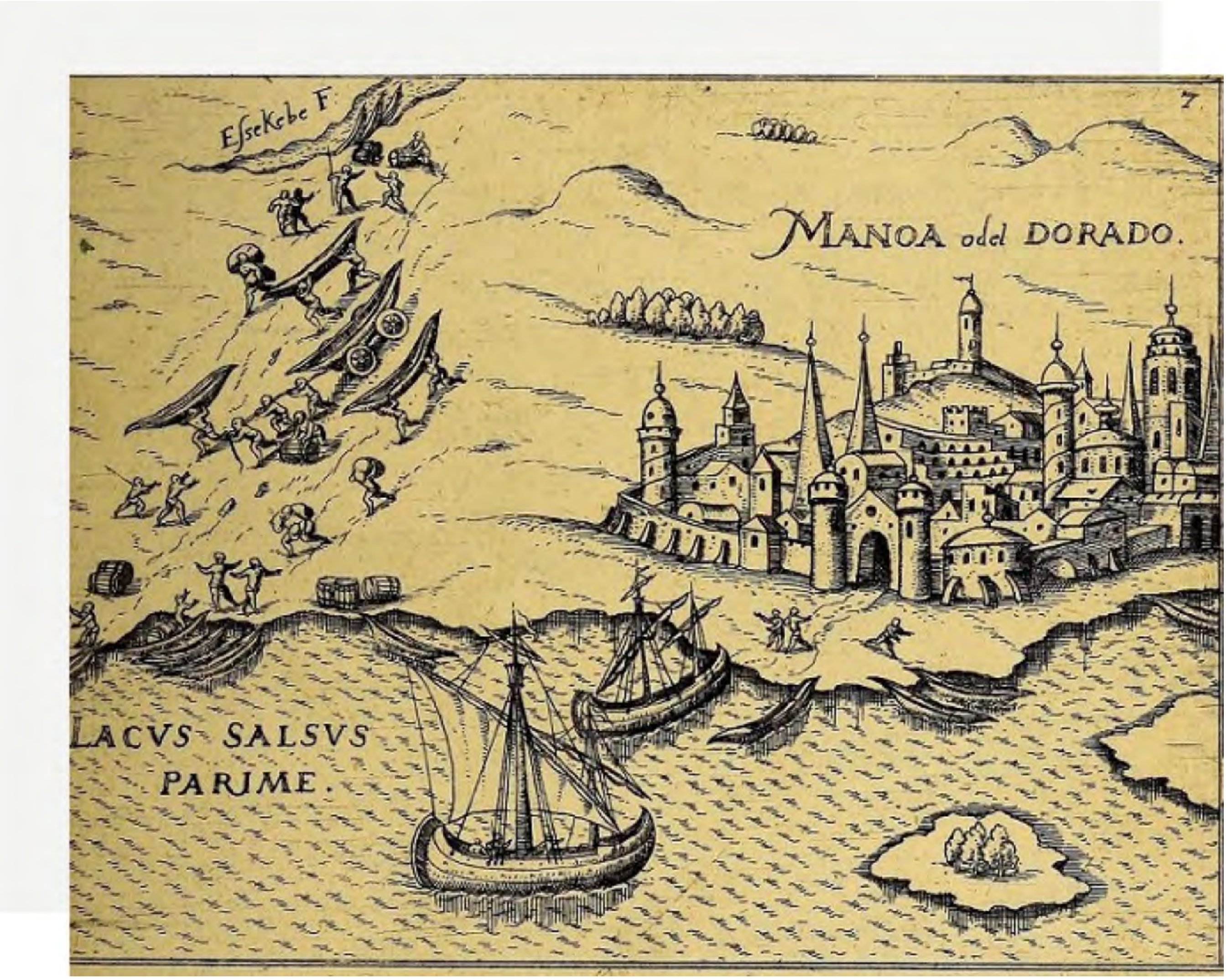

Figure 9.4 The city of Manoa or El Dorado on the shores of Lake Parime. Source: Ralegh (1848).

as those of the Spanish adventurer Pedro Bohórquez, who supposedly arrived at the capital of Enim in 1635 and met its sovereign in the royal palace. During the 1680s, the missionary Manuel Biedma founded three missions that provided the necessary infrastructure for the exploration of the upper Ucayali River, where that kingdom was supposed to be located (Santos 1992: 138).

The fantastic coexisted with the possible, always with the certainty that the Amazon had potential for extractive activities. The river was also considered the boundary between the island of Guyana to the north and the island of Brazil to the south, with the island of Brazil's southern limit the La Plata River (Ibáñez Bonillo 2015).

One expedition in search of the Country of Cinnamon was led by Gonzalo Díaz de Pineda, who left Quito in 1538. They only reached the foothills. Shortly after, Francisco de Orellana's expedition took place. Narrated by Gaspar de Carvajal, his chronicle was crucial for the construction of images of the inhabitants of the forests, among them the legend of the women warriors. El Dorado appeared in narratives from the 1530s (Langer 1997). Its alleged existence led explorers to several places: the mountains of present-day Colombia, Ecuador, and Peru; the Amazon; and sites in Central and North America. Was El Dorado an Indigenous ancestral myth, or was it created to mock, confuse, or get rid of the oppressors? Did it only exist in the imagination of Europeans, to accommodate and justify their wishes and expeditions? The answer perhaps lies in an amalgam of these and other possibilities. What we can be sure of is that Europeans named the place with words familiar with their symbolism and their ambition for gold. One of the best-known narratives in this regard dates back to the 16th century. Walter Ralegh, who entered from present-day Guyana in 1595, wrote an account of a vast, rich, and beautiful empire, whose capital, Manoa, was El Dorado (Figure 9.4). His tale contained fantastic ingredients to stimulate England's imagination and greed, among other things claiming that it was a continent isolated from the rest of America (Ralegh 1848).

During the second half of the 16th century, several Spanish expeditions departed from Cusco and Asunción in search of the Kingdom of Paitite or Mojos. From Cusco they reached the region of Madre de Dios and the Beni River, and reported numerous Indigenous peoples living in the foothills, whom

Figure 9.5 The Amazon River, 1691. Source: Fritz (1691).

they generically called *chunchos*. Those that left Asunción founded places such as Santa Cruz de la Sierra in 1561, and went to the land of the Mojos Indigenous peoples, in the upper and middle Basin of the Mamoré River, without finding the wealth they were looking for. A well-known expedition of that time, because of its dramatic circumstances surrounded by treason and murders, was that of Lope de Aguirre.

From 1640, expeditions included new goals and activities, including missionary purposes (Saignes 1981). Several religious groups, especially the Jesuits and Franciscans, incorporated cartography and natural history into their activities, helping to spread the idea of a wonderful world and providing instruments for its control (Chauca 2019). In 1741, the Spanish Jesuit Joseph Gumilla published the book *El Orinoco Ilustrado*, describing the preparation of *curare* poison and giving accounts of Amazonian peoples and nature. When the French academic Charles Marie de la Condamine traveled the river with the Riobambeño Pedro Vicente Maldonado, in 1743, he met the Swiss Joannes Magnin, a cartographer and ethnographer in charge of the missions of Maynas, who gave him copies of his maps (Condamine [1738] 1986). The academic also accessed at least one map by the Czech-German Samuel Fritz (Figure 9.5), who lived in the region in the late 17th and early 18th centuries (Almeida 2003). He took these maps to Europe and used them to perfect his own drawings. Pedro Maldonado contributed to the knowledge of the Amazon through his fine map of the Real Audiencia de Quito and his lectures on the poison called *curare*, a mixture of various ingredients, before the Académie Royale des Sciences in Paris in 1747, and the Royal Society in 1748.

A singular and unusual narrative of the Amazonian journey was that of the Riobambeña Isabel Godin des Odonais. In 1750, her French husband Jean Godin des Odonais, nephew of the academic Louis Godin, arrived in Quito as part of the Geodesic Mission together with La Condamine and other academics. He traveled to Cayena without his wife and could not, or did not want to, return to Riobamba (present-day Ecuador). More than 20 years later, she departed to Cayena, crossing the Amazon, and had a dangerous and dramatic journey in which her companions died, leaving her alone. On the brink of death, she was helped by two Indigenous people. Seeing her alone and lost in a riverbank, they helped her embark in a canoe, gave her all the attention needed to heal, and took her to Andoas, from where Isabel was able to continue. That adventure, recounted in the Amazon, in Cayena, and in the salons of Paris by Isabel and her husband (Godin des Odonais [1773] 1827), spread around the world and contributed to the myth of a dangerous territory.

A geopolitically-relevant expedition in the mid-18th century was the demarcation of the Treaty of Madrid (see next section). In 1754, the Spanish crown sent a commission under José de Iturriaga with officers, doctors, cartographers, astronomers, chaplains, surgeons, soldiers, and a group of naturalists led by the Swedish Pehr Löfling.

Among scientific explorers of the Amazon, two that stand out are the Prussian Alexander von Humboldt and the French Aimé Bonpland. They confirmed the veracity of the imaginary “island of Brazil,” when verifying that the Casiquiare channel joins the Rio Negro to the Orinoco River (Figure 9.6). They also made novel observations on Amazonian fauna and flora, such as electric eels, on which experiments were performed (Figure 9.7) (Humboldt and Bonpland 1811-1833).

For Europeans, the Amazon always represented an exotic territory with countless unknown riches, promoting all kinds of myths. Early raids sought, with the force of the sword, everything from precious metals to slaves. They established the first narratives about a space that could be cruel, although still holding rewards. Missionaries became key to knowledge circulation and territorial control, being the protagonists in the opening of waterways, drawing of maps, and ethnographical and natural history observations. They were followed by naturalists motivated by curiosity and economic interests, sponsored directly or indirectly by hun-

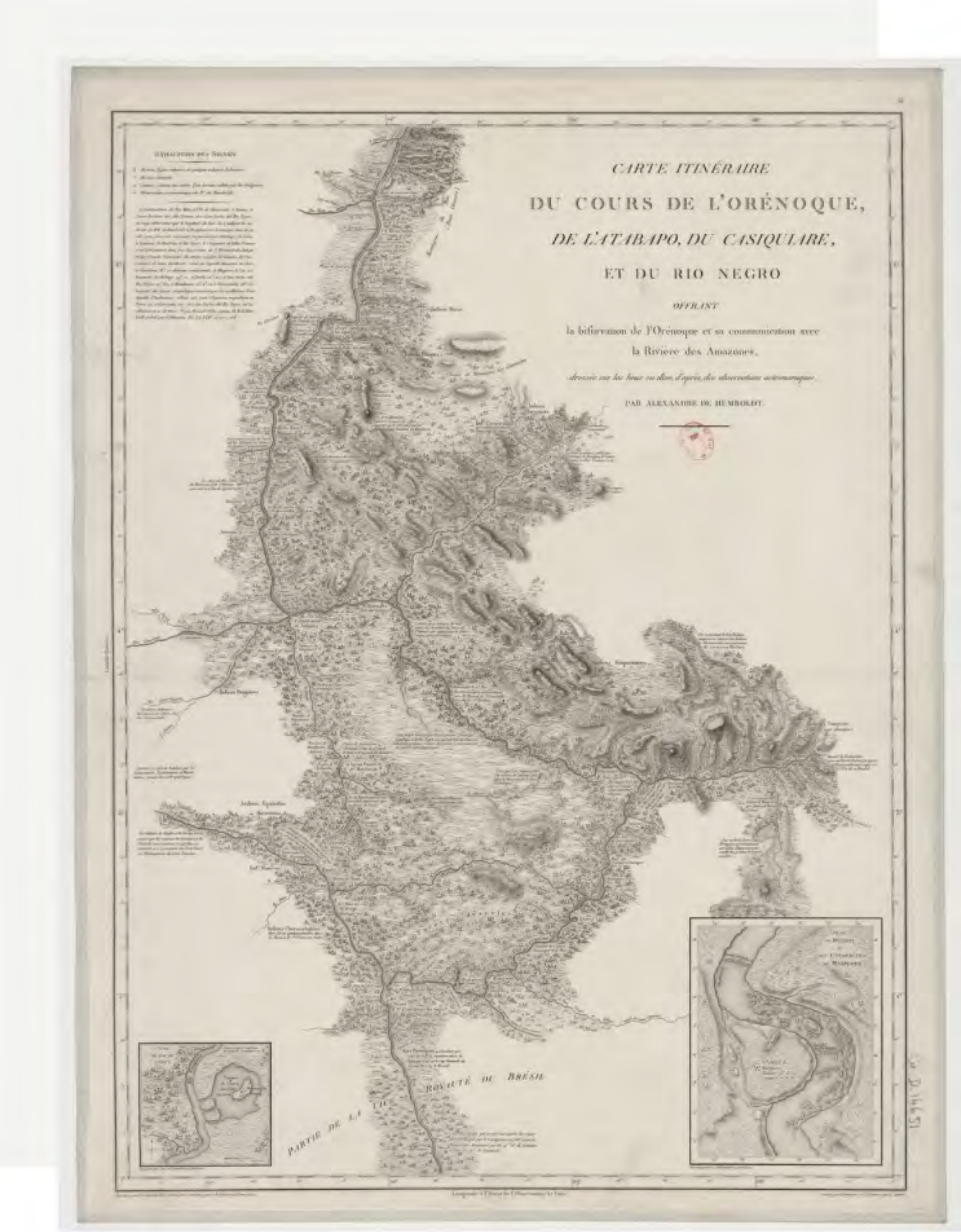

Figure 9.6 The Orinoco, Atabajo, Casiquiare and Negro River, 1800

ger for overseas territories and raw materials. Occasionally, these actors refuted or clarified myths, but always built new challenges for scientific curiosity, maintaining fascination for a territory rich in possibilities and risks. These fantastic visions of a place containing wealth, and knowledges about the material and cultural world are still very alive.

9.5 Conflicts between the Kingdoms of Spain and Portugal

The Lusitanian–Hispanic confrontation is almost as old as the arrival of Europeans in America. While Pope Alexander VI's Inter Caetera Bull, issued in 1493, donated the American territories to the Catholic Monarchs, in exchange for the spread of Catholicism among "their" native populations, the Treaty of Tordesillas (1494) gave the Spanish crown control over the entire continent, except for the far east which remained in Portuguese hands (Figure 9.8). The territorial agreement did not guarantee dominion over most of the Amazon, much less its inhabitants (Herzog 2015a: 17-37), but undoubtedly laid the foundations for what would end up being the current configuration of the region and, by extension, the majority of South America.

The absolute lack of knowledge of the territories crossed by the imaginary demarcation line meant that the Treaty of Tordesillas was not easy to apply. Both crowns vowed to respect this delimitation, but the tools each empire used in its penetration process and the obstacles each one faced explain the differences in their expansive success. Whereas the occupation of the Amazon received broad support on the Portuguese side, the Spaniards governed as though tropical frontiers were worthless (Lucena 1991: 7). The Portuguese advancing forces included soldiers and ransoming troops, allied natives, missionaries, and private traders, whereas those of the Spanish consisted mainly of missionaries and, to a lesser extent, soldiers. Hence, where the principal frontier institution in one kingdom was military, in the other it had an evangelistic character. Moreover, the Spaniards' incursions into the Amazon were short-lived and without continuity over time, therefore failing to consolidate a permanent presence. Simultaneously, the Lusitanians made uninterrupted advances from their coastal settlements to the west, ascending the great river and its tributaries beyond the line agreed upon in the treaty, strengthening their presence in the tropical plain (Zárate Botía 2001: 236-240).

The Portuguese exploited the dynastic union of the two Iberian crowns, between 1580 and 1640, to push their conquests far to the west (Hemming 1978: 229). Using a military, religious, and administrative project for the Basin, they laid "the foundations for the integration and effective colonization of the immense Amazonian territory" (Santos Pérez 2019: 45). Agents from both kingdoms spread the Portuguese and Spanish languages and imposed European practices (cultural, commercial, legal, spiritual) that would guarantee colonization; we will delve into that later. It was in that context that Pedro Teixeira's expedition in 1637–1639 took place. His travel up the Amazon River to Quito sought to integrate the space dominated by both crowns, recognize the territory and Indigenous populations, and confront English, French, and Dutch occupation attempts from the north (Hemming 1978: 213, 223-237). In any case, border conflicts resumed almost immediately after the separation of the so-called "Iberian Union" in the mid-17th century.

The limits between Portuguese and Hispanic possessions were still far from defined at the beginning of the 18th century. Border conflicts intensified between both crowns. The dynasty that assumed the Lusitanian throne strengthened the model that had been in place since the previous century to ensure a vast presence of its various colonial agents in the Amazon. Over the following decades, more fortifications were built on the northwestern and southwestern flanks of the frontier with the Spanish. Also, exploration by religious orders was encouraged up Amazonian rivers until they converged in the territories that, in turn, were occupied by missions of their counterparts under Spanish jurisdiction. Moreover, the advance of the

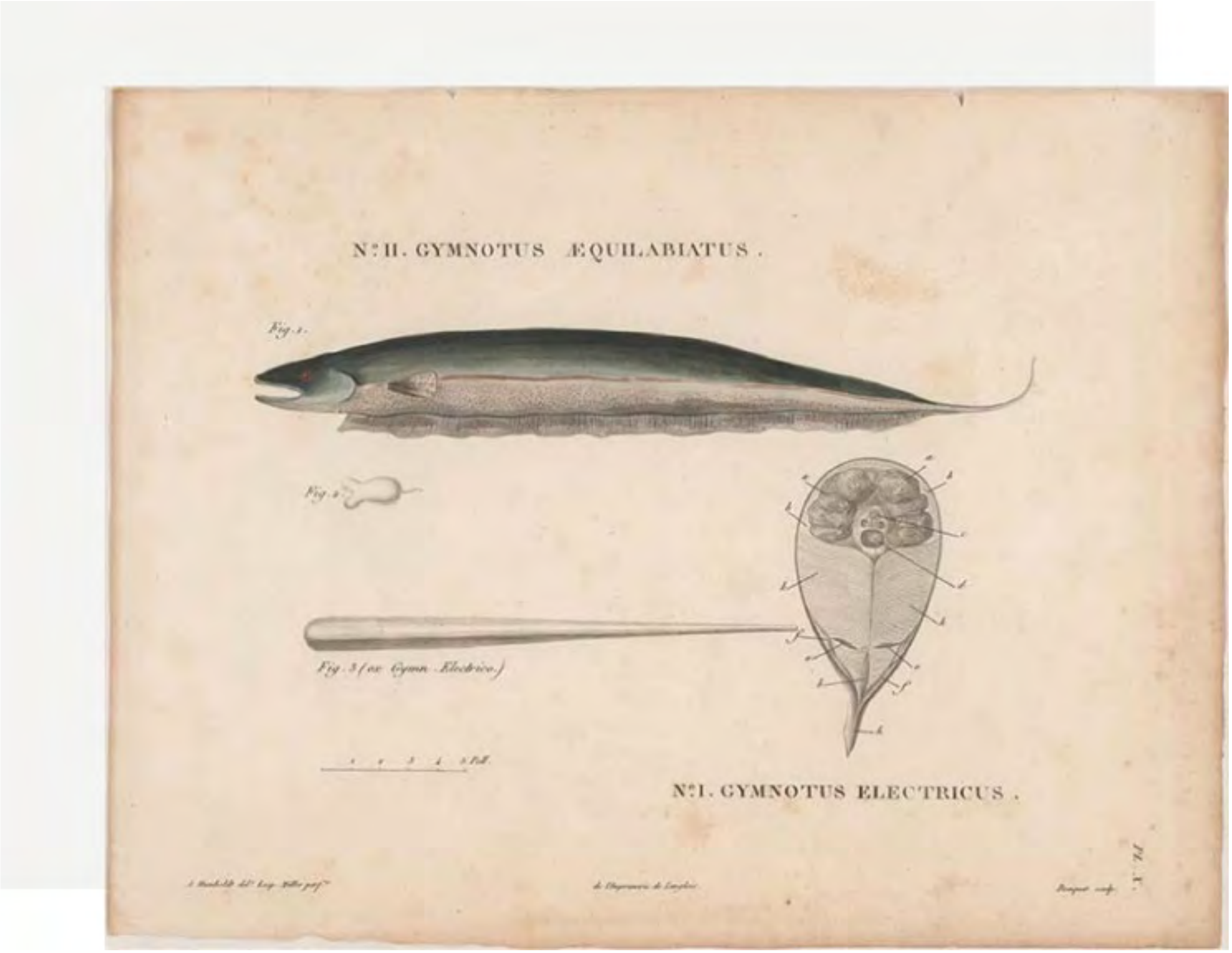

Figure 9.7 A cross-section of the electric eel (lower right) and an elongated knifefish (top). Source: Humboldt and Bonpland (1811-1833).

agricultural frontier required Indigenous labor captured by ransoming troops and private individuals with (and without) a royal license (Hemming 1978: 217-282, 416-451; Purpura 2006). This expansionist policy resulted in increased *in situ* or diplomatic disputes (Herzog 2015a) between state, clergy, and military agents; traders; and Indigenous people, particularly in the areas of the Guaporé, Mamoré, Marañón, and Napo rivers (Lehm Ardaya 1992; Avellaneda 2016; Lopes de Carvalho 2011). The reaches of Teixeira's and other ransoming expeditions led the Lusitanians to place the western border with the Spanish at the mouth of the Yavarí River (Hemming 1978: 275; Santos-Granero 1992: 168).

In the mid-18th century, pressure to end long-standing disputes made the boundary demarcation between the two crowns an urgent issue. The Treaty of Madrid (1750) was approved after several negotiations in which each party provided maps, documents, and reports to support its arguments (Ferreira 2007; Martín-Merás 2007). This agreement modified the ambiguous demarcation line established three centuries earlier to another that was equally imprecise; although the treaty advocated the physical limits of the great tributaries of the Amazon River, such as the Yavarí, Yurúa, Purús, Guaporé, and Madera, their hydrographic basins were practically, if not totally, unknown. Therefore, the drawn borders linking these more

Figure 9.8 Boundary agreements between Spain and Portugal. Source: Own elaboration from Roux (2001).

or less known natural accidents were virtual. The treaty, however, was short-lived as it was voided in 1761 due to continuous incidents involving agents of both parties and intense smuggling between the two territories (Lucena 1991: 11-19; Roux 2001: 515-517). The lack of a recognized delimitation favored Portuguese advances towards the Neogranadine provinces in the north and Mojos and

Chiquitos in the south, with the consequent dispatch of armed forces by the Spanish authorities. Meanwhile, the military, administrative, and economic reforms undertaken by both crowns since the mid-18th century promoted the furtive migration of missionary Indigenous, enslaved or free African people, farm laborers, and deserting soldiers between both domains (Lopes de Carvalho 2011; Santos Gomes, 2002; Avellaneda 2016; Martínez 2020). The said scenario compelled the opening of new diplomatic negotiations between Spain and Portugal that finally gave rise to the Treaty of San Ildefonso in 1777 (Figure 9.8). This agreement reproduced the terms of 1750, specifying certain legal aspects and maintaining many of its geographical uncertainties (Lucena 1991: 24-28; 1999; Torres 2011; Herzog 2015a: 25-69).

The delineation of borders on the ground involved Boundary Commissions composed of engineers, geographers, botanists, and astronomers appointed by each crown (Hemming 1987: 26-35). Several commissions, a priori composed of an equal number of Spaniards and Portuguese, worked along different areas of the demarcation line. However, in most of them, the disparity between the Spanish and the Portuguese expeditions with regard to personnel numbers, logistics, and control of supplies and provisions, would subordinate the former to the latter's interests. This situation eventually led to the legitimization of Portuguese dominion over many of the disputed areas (Lucena 1991; 1999; Zárate Botía 2001: 250-255). These commissions' negotiations and delimitation work were substantially responsible for the current configuration of the Amazon by "outlining and creating an imperial frontier that did not exist until then, and by giving shape to what is known as the Andean Amazon or upper Amazon, and the Brazilian Amazon" (Zárate Botía 2012: 29).

9.6 Depopulation: The impact of conquest and colonization on Indigenous peoples

As mentioned in Chapter 8, the demographic loss of Indigenous populations estimated in the first 100 years of conquest and colonization of the Amazon reached up to 95% (Koch *et al.,* 2019). The high vulnerability of these peoples to inter-ethnic contact continues to the present day owing to the rapid spread of diseases and a fall in fertility rates (Morán 1993). In the 1950s, anthropologists were concerned with the demographics of Indigenous populations in Brazil. Ribeiro (1956) and Wagley (1951) noted that contact with non-Indigenous peoples has led to demographic catastrophes, in many cases even to ethnocide. Between 1900 and 1957, 87 ethnic groups had become extinct in Brazil alone (Ribeiro 1967). At present, Indigenous peoples in initial contact or in voluntary isolation face the risk of disappearing because of the same causes.

Analysis of demographic evolution of Amazonian populations in the 16th to 17th centuries relies on data collected in response to various criteria and positions on the potential of ecosystems and the workforce. It also builds on estimates of chroniclers and missionaries made upon direct observation or by transmission from their informants. In contrast, the recording of missionary data for administrative and evangelization purposes was relatively more systematic in the 18th century.

According to archaeological evidence (Chapter 8), pre-colonization demographic densities of Indigenous populations were higher than those today. These findings have led to attempts to estimate, in some way, the demographic losses caused by contact with Iberian agents during centuries of conquest and colonization. One of the first researchers to link archaeological remains and demographic losses during the first century of contact was William Denevan (1980). In his opinion, estimations made before 1950 and based on sources from the second half of the 17th century underestimated Indigenous populations in the Amazon (Steward 1948), as by this time Indigenous peoples had already suffered the onslaught of disease and epidemics as a result of contact. In addition, scholars extrapolated these data to the entire Amazon, but Denevan pointed out that the demographic distribution was very uneven, with areas with very high densities on the banks of the great rivers (*várzea*), the coast at the estuary in the Atlantic, and the low savannas. However, new archaeological discoveries indicate the existence of many other regions that must have had high population densities. In all cases, it is estimated that Indigenous populations before contact were far higher than today (Denevan 1980). Depopulation implied processes of ethnic disarticulation that accentuated the vulnerability of Indigenous peoples, forcing them, in many cases, to seek refuge and even request the presence of missionaries and the establishment of reductions in their territories (Lehm, 1999; 2016).

As discussed at the beginning of this chapter, the first chroniclers, such as Gaspar de Carvajal, observed numerous Indigenous populations governed by complex organizational systems and enjoying products and resources in abundance. A century later, Cristóbal de Acuña already accounted for the disappearance of once populous Indigenous peoples, such as those who lived at the Amazon's estuary in the Atlantic and the Omagua regions (Carvajal [1541-1542] 2007; Carvajal, Rojas y Acuña 1941:111). Understanding the shocking period of conquest on a demographic level demands a greater emphasis on the study of sixteenth-century sources.

More systematic demographic information is available for the second half of the 17th century, because it was in the interest of missionaries and the Spanish crown to keep relatively detailed records on demographic dynamics. Similarly, in the Pará and Maranhão regions (Brazil), epidemics were documented out of concern for loss of Indigenous and slave labor. There are several references to demographic losses because of the spread of diseases, facilitated by the concentration of Indigenous populations in missions, as well as to the damage caused by displacement. Raids were conducted to capture Indigenous populations and subjugate them to labor regimes and life systems contrary to their own traditions.

In some Jesuit and Franciscan missions (Table 9.1, Figures 9.9 and 9.10), initial increases in population resulting from Indigenous recruitment later led to progressive demographic declines in the second half of the 18th century. They recovered slightly and steadily until the rubber boom of the late 19th century. Indigenous populations would never fully recover from the impact of conquest and colonization.

Indigenous peoples located in the sub-Andean region were the most affected, owing to their proximity to Spanish cities. As colonial rule expanded, so did the diseases brought by Europeans (smallpox, measles, and influenza), against which native populations lacked biological defenses. The Panatahua and Payanzo peoples from the Franciscan Conversions of Huánuco, in Perú, decreased from 10,000 inhabitants in 1644 to only 300 in 1713 (Santos-Granero 1992: 184). Their Amazonian ethnic identity would disappear as they became subsumed into the Andean population. As noted, the disappearance of many Indigenous peoples from the eastern foothills caused fractures in relations between the Andes and the Amazon and fed the idea of a "natural frontier" and a "great Amazonian emptiness."

The Iberian conquerors used the great rivers to enter the Amazon, spreading disease among the numerous Indigenous populations that lived there. The population was concentrated in missions, creating the conditions for the spread of disease, as in the case of the Maynas region. Indigenous peoples suffered significant demographic losses and many nations disappeared. Between 1719 and 1767, the region was devastated by three great epidemics that affected the Maina, Cocama, Cocamilla, Omagua, Yurimagua, and Conibo peoples, concentrated in missions along the rivers Marañón, Huallaga, Ucayali, and the upper Amazon. Demographic losses were extensive; for example, the general smallpox epidemic of 1680–1681 killed approximately 85,000. Of the 100,000 individuals concentrated in the missions of Maynas, only 15,000 survived (Santos-Granero, 1992: 189). The continuous recruitment of independent groups explains the regular increase of the population in the missions of Maynas; there, the Jesuits benefitted from so-called *correrías*

Table 9.1 Census reports from Maynas. Source: Golob (1982:193), in: Santos (1992: 186).

Year	Number of Indigenous peoples	Number of missions	Population average per mission
1719	7,966	28	284
1727	5,942	22	270
1740	11,036	32	313
1745	12,909	41	307
1760	12,229	34	359
1767	19,234	36	534

de indios (Indian raids) in the interfluvial regions to recruit Indigenous populations to the alledged "safety" of missions (Lehm 1992). Both in the missions of Maynas and the Conversions of Huánuco, the under-5 population was the most affected; in some missions, during a four-year period, no child survived to age 5 (Santos-Granero 1992: 190).

The demographic evolution of five Amuesha missions in the Franciscan conversions of Cerro de la Sal (Peru) (Figure 9.9) and twenty-six Jesuit missions of Mojos show similar trends (Figure 9.10). Early demographic growth was mainly due to recruitment, followed by demographic drops that reached 50% compared with the peak, and finally a recovery process. In the Cerro de la Sal Conversions, demographic declines were mainly owing to the spread of disease and, as discussed later and by Santos-Granero (1992), subsequent uprisings. From 1710 to 1818, these missions suffered significant epidemics; between 1721 and 1723 the so-called black plague affected mainly the Asháninka, and between 1736 and 1737 influenza devastated the Yánesha and Asháninka (Santos-Granero, 1993). In Mojos, according to Block (1994), demographic declines were owing to the impact of disease, low fertility rates probably due to contact stress, cultural practices such as selective infanticide to the detriment of women and twins, and Lusitanian invasions. The size of the population makes it possible to highlight the importance of the Mojos Missions in comparison with those of Cerro de la Sal, and even those of Maynas.

The regions of Pará and Maranhão also suffered epidemics in 1661, 1695, 1724, and 1743–1749. The smallpox explosion of 1661 occurred in Pará; it began among the Portuguese settlers, affecting them, their slaves, and the Indigenous populations of the interior villages. In 1695, an outbreak of smallpox spread by a slave ship in Maranhão was known as the "great death," with over 5,000 lives lost by the end of the century. Between 1724 and 1725, a new epidemic caused a massive number of deaths. More than 1,000 slaves died, particularly Indigenous peoples. The cause was a visit from the bishop of Maranhão and Pará. The first cases appeared among those who traveled in the canoe transporting them, and along their journey they left sick Indigenous people in the villages they visited. Many Indigenous people fled to the interior seeking refuge, taking the disease with them to regions where the magnitude of its impact will never be known. Between 1743 and 1749, epidemic outbreaks of smallpox and measles were registered in Pará and all its districts. In 1750, known deaths from this long period of epidemics reached 18,377, of which 7,600 were residents of Belem and the rest of Indig enous villages subject to religious orders (Chambouleyron *et al.,* 2011).

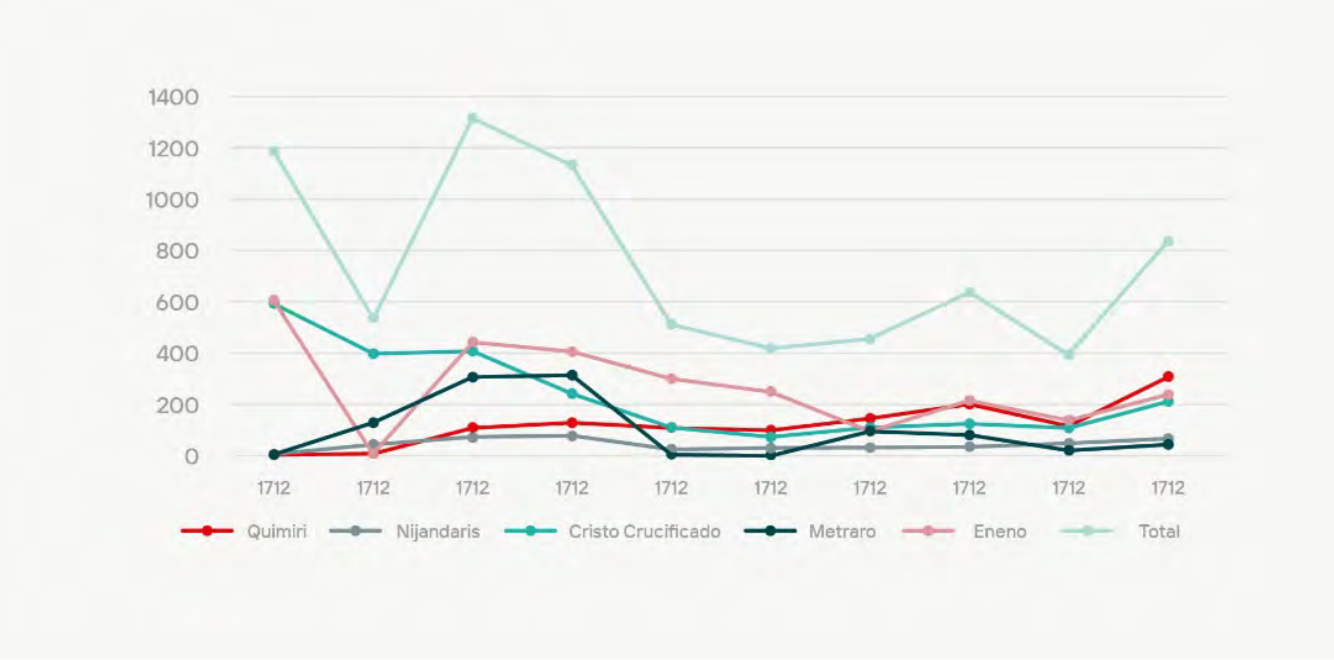

Figure 9.9 Demographic evolution of Amuesha in Cerro de la Sal Conversions, 1712-1762. Source: Santos (1992: 194).

Figure 9.10 Demographic evolution of Mojos Missions, 1691-1832. Source: Barnadas (1985: LV).

In the Portuguese Amazon, demographic losses due to epidemics resulted in royal authorizations to "extract" free people from the forest to replace labor force losses in cities and settlers' agricultural areas. Likewise, declines due to epidemics resulted in the intensification of the slave trade from Africa to Pará and Maranhão. The first slave route to this region developed between the mid-1690s and the mid-1700s. After 1690, the losses suffered as a result of epidemics led to the recruitment of people to serve as soldiers, especially from the interior regions of the Madera River Basin (Chambouleyron *et al.,* 2011).

Expeditions and Boundary Commissions resulted in new demographic declines owing to confrontations with the Indigenous peoples and the spread of disease. During the first half of the 18th century, confrontation between the Portuguese and Manao caused the death of more than 20,000 of the latter. By the second half of the century, they had been decimated. However, some survivors joined the Mura, putting up the greatest resistance to Boundary Commissions (Zárate, 2014).

In summary, there were two major periods for demographic analysis; first, the arrival of the conquerors, whose references are qualitative and not very precise; and second, the colonial period, whose data is based mainly on more detailed mission records, but with limited data on other areas. Additional sources are the reports of Portuguese authorities based in Belem and Maranhão.

9.7 Colonial control and dominance through the settlement of European populations

In the 16th-18th centuries, the Amazon became an open field for different agents who entered the region to exploit its natural, mineral, and human resources; to establish settlements, including urban centers and missions; and to evangelize its inhabitants in the name of the unity of the Christian faith (García Jordán 1999). During this period, uncultivated spaces were seen by Europeans as unoccupied, or physically abandoned, open, and available for occupation despite the presence of Indigenous people (Herzog 2015b). Accordingly, they believed that by establishing a population and economic activity the land was controlled, and therefore under colonial rule.

As described above, the first explorations were made primarily by Spaniards looking for mythical riches. The Spanish Crown delegated conquest to private citizens, promising titles and grants to those who were successful. These so-called *huestes indianas* had an eminently military character and their objective was to discover new territories, identify their resources, make contact with the native population, and establish urban centers (Useche 1987; Renard-Casevitz, Saignes and Taylor, 1988: 124-179, 233-293).

The most important institution introduced by the Spanish monarchy to ensure control was the *encomienda*, a process by which The Crown gave Indigenous populations within a specific territory to individuals who had excelled in military service. The *encomenderos* did not have rights over the land, but rather over the populations, regrouped in new settlements, indoctrinated in the Christian faith, and transformed into vassals to be used as labor. Although the *encomienda* had a greater presence in coastal and highland areas, it also spread to the Amazonian foothills, especially Ecuador (Renard-Casevitz, Saignes and Taylor, 1988:233-293; Santos 1992:81-106, 157-163). Lack of regulation led to rampant violence and abuse by the *encomenderos*. The publication of the *Sublimis Deus* Bull, stating Indigenous peoples had the right to be treated like any other vassal of the Christian princes, prompted a change in legislation, including the prohibition of inheriting people. This institution slowly disappeared as the *encomenderos* died, leaving the natives under the tutelage of the Crown (Peñate 1984). However, Taylor (1999: 214) points out that the titles and privileges that went with them were recognized in the western Amazon for many years to come. From the 17^{th} century onwards, use of the military for conquest declined in favor of a peaceful, non-warlike occupation by missionaries, as will be shown in the following section. However, this did not exclude the use of force on certain occasions (entries or raids), either to face native hostility or to ensure evangelizing on the immediate border with other European crowns (Herzog 2015a: 109-114). Indeed, the English, French, and Dutch also settled between the estuaries of the Orinoco and the Amazon, competing with their Iberian rivals for trade relations with Indigenous peoples (Hemming 1978: 119-138, 198-229, 283-311; Lorimer 1989; Van Nederveen Meerkerk, 1989).

In the early 16th century, the Portuguese established small warehouses along the Atlantic coast where people lived and occasionally traded with Indigenous people. Soon after, the Crown sought to expand its domains, dividing the coast into hereditary captaincies whose administration was granted to private individuals who, in turn, distributed land to their men. Armed expeditions, known as *bandeiras*, were organized from these captaincies to advance towards the interior in search of gold, precious stones, and slaves for the coastal enclaves and plantations. The northernmost captaincy lay to the east of the estuary of the Amazon. The Portuguese attempted to explore the great river early on, but Indigenous resistance to the advances of ransoming troops soon halted their efforts in the area for the rest of the century. Slaving expeditions to the Pará and lower Amazon restarted in the 17th century, now with the assistance of missionaries. Those captured were classified as slaves, and those who were "persuaded" were considered as "free;" the former belonged to the traders and settlers, the latter were lodged in missions and expected to work for private individuals and state officials (Hemming 1978: 7-10, 69-78, 184, 218-220, 335, 412-413; Monteiro 2019).

Several attempts were made to free Indigenous people under Lusitan rule; none lasted. Indigenous capture and enslavement continued to be legally enforced throughout the colonial period, and The Crown did not interfere with the capture of slaves (Hemming 1978: 311-317, 412-419; Perrone-Moisés 1992; Lopes de Carvalho 2019: 147). Slavery remained institutionalized during the dynastic union of the two Iberian crowns (1580–1640), despite the passage of laws protecting Indigenous people. This was partly because the Spaniards had promised not to change the Portuguese legal system, and felt the inhabitants of the Lusitanian kingdom did not fit into the Laws of the Indies (Hemming 1978: 152), and partly because of the Portuguese' interest in securing control of Maranhão and Pará, a territory organized jurisdictionally as a connecting bond between the areas under the control of Spain and Portugal that approximately corresponds to the current Brazilian Amazon (Marques 2009; Santos Perez 2019).

Europeans associated the right to land with agriculture; hunting and gathering did not have a place in the equation. The Spanish crown respected the territorial rights of Indigenous peoples over the lands they cultivated, as long as they submitted to the kingdom's laws. In the 16th century, they were issued titles based on the continued use of those lands by their ancestors. Such documents would later be invoked to prove their rights to land since the "times of conquest" (Herzog 2013; 2015a: 124-125). However, this only benefited sedentary societies. The nomadism of most Amazonian peoples prevented legal recognition of the extensive lands they occupied and used (Mariluz Urquijo 1978). Agriculture and, thus, the settlement of these societies in a specific location, were essential aspects of colonial society.

Urban settlements (towns, villages, forts, and missions) were part of the colonial strategy of occupation and territorial control (Alencar Guzmán 2017). In the Amazon, disease, Indigenous resistance, and the lack of mineral wealth hindered the establishment of new urban areas. Current cities, such as Belèm do Pará or Santarém, remain in their original location. Many others moved, trying to find less problematic or richer places whose resources would not be depleted so easily, such as Santa Cruz de la Sierra in present-day Bolivia or Zamora and Archidona in present-day Ecuador. Others simply disappeared over time. In Spanish America, several towns founded in the late-16th and early-17th centuries became gateways from which all expeditions attempted to conquer the jungle until the late-19th century (Useche 1987; Renard-Casevitz, Saignes and Taylor, 1988: 124-179, 233-293; Musset 2011, 166). On the Lusitanian side, military and private agents progressively moved along the Amazon and the Tocantins rivers, and their tributaries, impelled by growing economic demands for resources and slaves. The location of savannahs on the banks of the great central rivers favored the formation of large cattle ranches and the expansion of agriculture based mainly on cocoa, tobacco, and sugar cane. The workforce of these plantations were primarily native and African slaves who arrived in the region in the mid-17th century. Their presence in the Amazon significantly increased agricultural production for export. Slave labor was also employed in the construction of urban public works and fortifications (Hemming 1978: 343, 367-376; Chamboleyron 2014; Sommer 2019: 617-618). In the 18th century, the last colonial urbanization processes took place in the Amazon, this time with a military feature; numerous fortifications were built to defend imperial borders against rival kingdoms (Souza Torres 2011). Likewise, Boundary Commissions contributed to this process; small, riverside villages ended up becoming cities, such as Barcelos in present-day Brazil. Other places they settled became town centers, such as San Fernando de Atabapo in present-day Venezuela. So-called "twin" cities also emerged on either side of disputed borders, such as Tabatinga and Loreto de Ticunas, later Leticia (Zárate Botía, 2012).

Raids originated from these areas, particularly in Portuguese domains, and trade relations were also established with some populations not subjected to the colonial labor system. European markets were filled with so-called *drogas do sertão*: vanilla, wild cinnamon, sarsaparilla, nutmeg, urucú, indigo, various oils, resins, wood, cinchona bark, and others. In return, natives obtained metal axes, knives, weapons, and fishhooks (Solórzano 2017: 197). Interest in metal tools led many of them to seek contact with colonial agents and even to appropriate forging technology. Access to metal sources also reinforced inter-ethnic conflicts and slavery relations between groups far from the trading front. Greed for tools created trade circuits connecting the upper Amazon with the Orinoco Basin in present-day Venezuela and the coasts of the Guianas. The exchange of slaves for tools intensified in the 17th and 18th centuries and lasted well into the 19th century (Benavides 1986, 1990; Santos 1988; Santos 1992: 5-32).

Alliances among European agents and Indigenous peoples shifted and became functional to the interests of both. Indigenous people expected gifts, involvement in trade circuits, titles recognizing their leadership, and dominion over rival groups in exchange for supporting European kingdoms. Europeans saw strategic allies in these autonomous nations, as they could serve as auxiliaries in expeditions into the jungle, act as intermediaries, and convince independent peoples to negotiate with them. Alliances allowed the expansion of colonial agents (traders, missionaries, soldiers, ranchers, miners), and extractive and agricultural industries (Herzog 2015a: 97-109; Roller 2019). It is worth recalling that under European colonial logic, such alliances, rather than securing friend- and partnership, formally turned them into vassals and the lands they occupied into the property of the Crown (Herzog 2015a: 95).

Incursions had a strong impact on native societies, causing disappearances or disruptions of many groups, as well as regional dislocations. The societies that suffered the most damage in the Spanish territories were those located in the foothills and high jungle, owing to their proximity to Andean urban centers. Among them, riverine groups were more affected, relative to interfluvial ethnic groups (Santos-Granero 1992). In Portuguese lands, the societies that inhabited the banks of the Amazon River and the estuary suffered the worst fate, enslaved by the agents of Belèm do Pará. Those who faced less European contact lived in the *sertão*, the inland forests, along the less traveled rivers, or on the waterfalls of its tributaries (Hemming 1990: 213-218; Sommer 2019: 614). In short, the more impacted peoples as a result of the European presence were those that inhabited the main access routes to the Amazon.

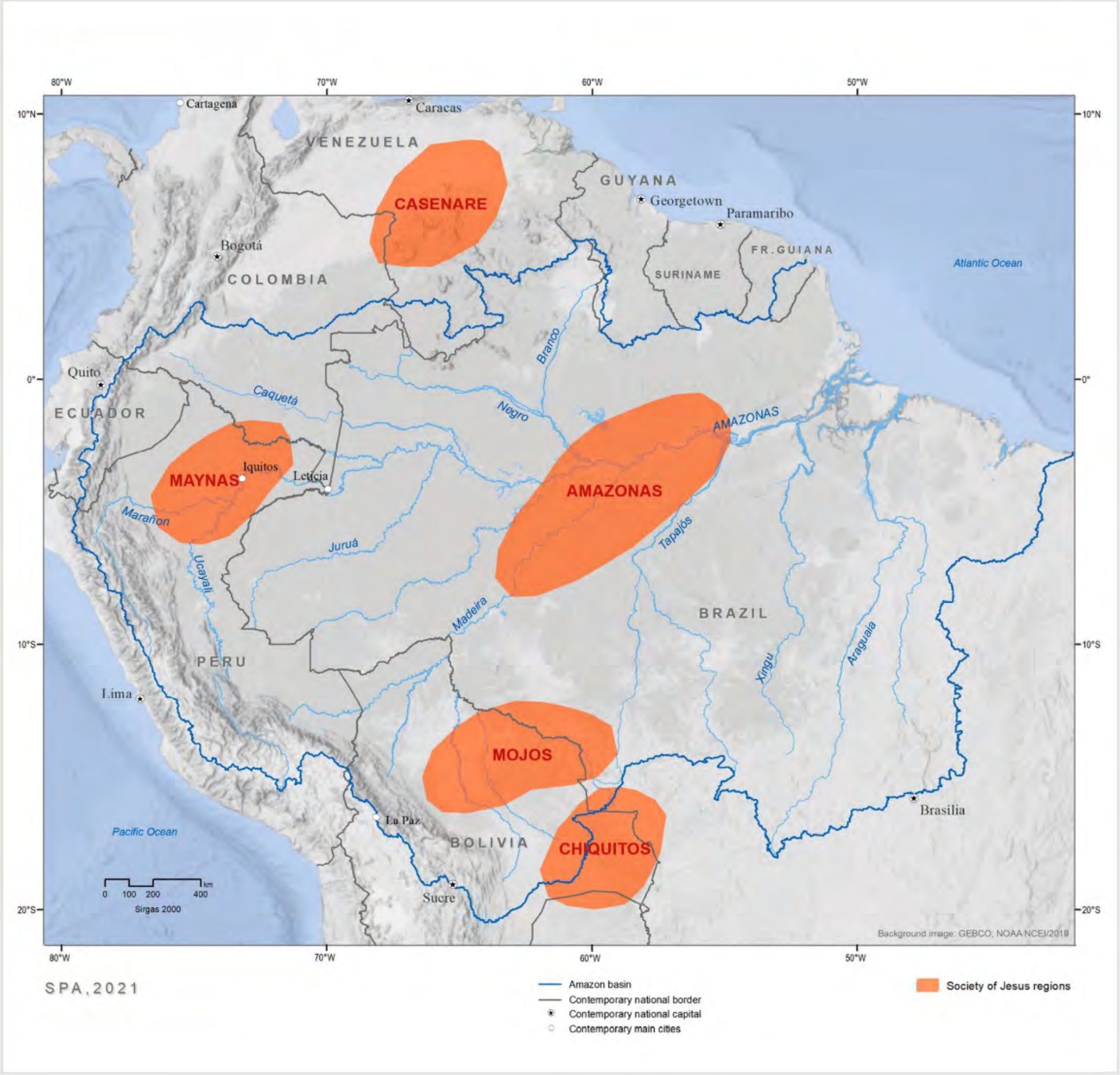

Figure 9.11. Society of Jesus in the Amazon. Source: own elaboration from Livi Bacci (2010).

9.8 Jesuits, Franciscans, and other religious orders

Cities were established by military and civilian agents to control territory, while missions aimed to evangelize Indigenous populations and bring them under the rule of the Iberian Crowns. Ordinances for new discoveries, conquests, and pacifications in 1573 provided that imperial expansion over these populations (and the territories they occupied) would be conducted using persuasion and appointed the mendicant orders responsible for such action. This norm was never revoked or modified, which is why it continued to be applied throughout the 18th century (Weber 2013: 144).

The first missionary wave took place around 1630. Dominicans, Augustinians, Capuchins, Carmelites, Franciscans, and Jesuits advanced towards the Amazon either from the Andes or the Atlantic coast. But it was the latter three that realized the largest presence in the region (Sweet 1995: 9-10). The Jesuits were the main agents of the Spanish Crown to enter the Amazon, in the upper Orinoco and the plains of Casanare and Meta, the Maynas area following the course of the Napo River, and the Mojos and Chiquitos regions in the headwaters of the Mamoré and Guaporé rivers (Negro and Marzal, 1999; Saito and Rosas, 2017). The intermediate areas from the Andean foothills to the Neogranadine jungles were assigned to Dominicans, Augustinians, and Franciscans (Santos-Granero 1992: 125-173; Merino, Olga; Newson 1994; Chauca Tapia 2019). Missionaries were of much less importance to the Portuguese, who delegated control of populations and territories to soldiers. The south of the Amazon River was assigned to the Jesuits, who operated in the valleys of the Madeira, Tapajós, Xingú, and Trombeta rivers, while the Franciscans settled in the North Cape (current-day Amapá). The Carmelites were entrusted with evangelization on the border with Maynas and the valleys of the Solimões and Negro rivers (Torres-Londoño, 1999; Alencar Guzmán 2017: 62; Sommer 2019; Lopes de Carvalho 2019: 136-137). The search for new populations to evangelize allowed the advancement of the internal border of both empires and the recognition of the geography and hydrology of the Amazon, giving rise to the early cartographies of these regions (Burgos Guevara 2005; Chauca Tapia 2015).

The missionaries' aim was the Christianization and Europeanization of Amazonian Indigenous groups, considered culturally and technologically inferior. Their lack of a stable and permanent place of residence, ignorance of the Christian faith, alleged poor discipline, and unfamiliar norms of behavior, at both the personal and group level, were perceived as signs of barbarism, justifying missionary intervention (Boccara 2010: 106-112; Waisman 2010: 209-211). The priority of the missionaries was religious conversion; the "infidels" received notions of catechesis to later be baptized and become "neophytes," that is, Christian people but in need of tutelage as they still had to learn to be "vassals" of the Crown (Saito 2007: 454). It was a religious guardianship to be conducted within the missions – that is, in an urban environment – where Indigenous peoples were to abandon their state of "barbarism" tied to life amid nature, embrace Western culture, and become "civilized."

The concentration of Indigenous populations meant the restriction of their mobility and autonomy, and the introduction of Iberian cultural aspects that were alien to them. The missions followed the Iberian "checkerboard" urban model, in which the church, workshops, and clergy residences were built around a large central square. Parallel streets were occupied by the dwellings of neophytes, while Indigenous catechumens (not yet baptized) lived on the periphery (Martins Castilho Pereira 2014). The introduction of new crops and cattle breeding caused changes in the landscape and ecology of the area (Radding 2008). The promotion of these activities sought to turn the neophytes into "productive subjects" through training in craft trades (e.g., blacksmithing, carpentry, spinning). This involved the introduction of a new concept of time, arranged according to a specific purpose and regulated by a bell; disciplinary aspects and a compulsory notion of work, leading to the rise of the idea of "indolence" for not producing what was expected; and last, the alteration of kinship systems, gender roles, and division of labor (Sweet 1995: 14-22; Santos 1992:43-44). The wealth produced by the missions did not always allow them to be self-sufficient. In the case of the Mojos, sumptuary goods, metal utensils, and the salaries of specialized personnel were financed with income obtained from slave labor on Society of Jesus estates located on the coasts of modern-day Peru and Ecuador (Block 1994: 65-77).

Various ethnic groups congregated at the missions. Europeans knew these peoples by the specific names of bands, tribes, and chiefdoms, usually given to them by those who did not belong to such groups. Chroniclers and clerics would assign multiple different names to the same people or apply the same name to several groups, depending on their location or relationship at any given time. These ethnic labels served more to ascribe an identity than to describe them, whilst suggesting a false sense of ethnic purity or continuity, ignoring that people met and mingled, entered and left groups, or became bilingual or polyglot (Weber 2013: 35). Indeed, as discussed in detail in Chapter 12, these populations spoke multiple languages, which prevented their evangelization. The missionaries tried to impose a *lingua franca* among Indigenous peoples, preparing standardized grammars and vocabularies, attempting a cultural and linguistic homogenization. The result of this policy was ambiguous; even though Quechuaization or Guaranization was achieved in some provinces, in others it was only possible to impose the use of a *lingua franca* within each mission (Lehm Ardaya 1992: 144-145; Pinheiro Prudente 2017). Over time, these languages solidified as specific idiomatic variants and became the identity mark of missionary ethnic groups (Wilde 2019: 549).

Figure 9.12. Peruvian Indigenous person with his weapons. Source: Eder (1791).

The highest authority within the mission was exerted by the missionaries. Indigenous leaders were recognized but subordinated to the supervision of the clergy. A new social order emerged. Native leaders held positions in government, ensuring community order (moral, social, productive), acting as auxiliaries to clergy in liturgical celebrations (as sacristans or musicians), and the militia, playing a defensive role against Lusitanian military advances.

The hierarchy of society within the missions gave rise to a new native bureaucracy. They were distinguished by their attire (clothing and accessories), differential access to resources and literate culture, education, and training in European arts such as music, drawing, and silversmithing (Saito 2007; Waisman 2010; Lopes de Carvalho 2011; 2019; Avellaneda 2016; Wilde 2019). New leadership emerged based on the authority and respect conferred by both Indigenous people and the missionaries, owing to their knowledge of Indigenous people and the appropriation of practices of Iberian origin (Sweet 1995: 36-39). Music, painting, and sculpture became the best vehicle for engageing Indigenous peoples in this new order, especially in the Jesuit missions. Conceptions and aesthetics of Indigenous origin were reflected in the arts, although subordinated to European creative logic, and perpetuated over time, even once the missionary process was over (Waisman 2010; Diez Gálvez 2017, Monteiro 2019).

The organization of missions entailed the territorial and demographic fragmentation of several ethnic groups, which were forced to leave their traditional lands to live under the standards of a new social, economic, labor, and political order, shaping new identities within the centers. Parallel to this process of deculturation, a course of ethnogenesis also took place. It was undertaken both by the missionaries; imposing institutions, knowledge, and habits; and by Indigenous peoples, adopting and appropriating them to suit their interests, and giving rise to the so-called "mission culture" or "missionary memory" (Block 1994; Wilde 2019). The experience of these Indigenous peoples led colonial agents, and later republicans, to consider them closer to "civilization", while groups that remained autonomous continued to be perceived and portrayed as hostile, barbaric, and savage.

9.9 Secularization of the missions

In the latter half of the 18th century, the Hispanic and Lusitanian monarchies implemented a reformist policy aimed at strengthening their respective kingdoms through the modernization and rationalization of the economy, society, and the administrative apparatus of both the peninsula and the Americas. The secularization of the missions pursued the integration of Indigenous peoples into a broader socioeconomic system, considering their submission to the general laws of justice and taxation; their insertion into labor markets, regional trade, and industry circuits; and their contact and mixing with colonial society.

The Jesuits were expelled as part of this reformist policy. Among the orders, they received jurisdiction over most of the Spanish Amazon. They exercised tight control over the neophytes under their tuition, ensuring their minimal relationship with the Hispanic colonial regime. They were also highly autonomous in the management and commercialization of supplies produced, making them appear as a threat to the power of the colonial state in the mid-18th century (Mörner 1965; Merino and Newson 1994). The Jesuit presence in the Lusitanian Amazon had been declining since the mid-17th century. Frequent conflicts between the missionaries, settlers, and soldiers for control of Indigenous labor strained the relationship of the former with the colonial administration. Their services would be requested and canceled on successive occasions by the governors of Maranhão and Pará, to the point of being replaced by the Carmelites at missions in the Solimões, Negro, and Branco River regions. This animosity would grow in the mid-18th century, as private and imperial interests in direct access to natural and human resources increased (Hemming 1978: 316-341, 410-461; Lopes de Carvalho 2019).

In Portugal, doctrinal modernization and the defense of royal rule advocated by Marquis de Pombal precipitated the estrangement of the Society of Jesus in 1759. In Spain, efforts to subordinate the religious orders reached its peak when Charles III expelled the Jesuits in 1767. France had already done so in 1764. At that time, the Society of Jesus served approximately 60,000 Indigenous people on the Hispanic Amazonian border in just over 70 missions, as well as 25,000 Indigenous people in ~20 missions along the lower Amazon and its tributaries in the Portuguese Amazon (Hemming 1990: 224; Merino and Newson 1994: 10-14).

In this context, the Spanish administration approved different provisions in each of its jurisdictions, with the aim of secularization, centralization, and acculturation of Indigenous populations. The fate of the Jesuit missions relied on their strategic importance, economic resources, proximity to markets, and temperament of Indigenous peoples. Those that still wanted to undergo conversion (neophytes) were handed over to the mendicant orders, particularly in areas connecting the Upper Amazon and the Upper Orinoco. Those who had already embraced Catholic principles and "learned" to live as Europeans ceased to be under guardianship and were recognized as full subjects of the Crown, for example those in the Guapore area. Their government was entrusted to civil administrators, while their spiritual affairs remained with the secular clergy (Merino and Newson 1994; Weber 2013: 162-201). In turn, in 1757 the Portuguese Crown enacted a Directorate to be observed in Indigenous settlements of Pará and Maranhão. Originally designed as a specific legislation for the

Amazon, it was soon extended to the whole Luso-American domain. Although it was devised as a temporary measure, it would be in force for 40 years. The Directorate withdrew all orders from direct control of the peoples concentrated in villages and the missionaries were assigned exclusively to contacting and converting "wild tribes." Former missions acquired township status and fell under the rule of a civilian officer, who was to oversee the administration and "civilization" of Indigenous peoples and secure their rapid and complete integration into Portuguese society as quickly as possible. It also meant the legal end of Indigenous slavery, although in practice it persisted for decades (MacLachlan 1972; Hemming 1987: 11-12, 40, 58-80).

Both crowns understood that exposure to daily colonial life was the optimal path to acculturation. Especially emphasized on the Lusitanian side, their aim was none other than the "Portuguese-ization" of the Amazon. Missions lost their native names and we re-named after towns in Portugal. The entry of settlers into old missions and their marriage to native women was encouraged to accelerate the adoption of western-style domestic and economic practices. The Portuguese language was imposed, and considered a fundamental basis of civilization (Hemming 1987: 12; Sommer 2019: 615-616, 620-621). In the Spanish domains, the use of Castilian within former missions intensified at the expense of native languages. Recognition of the monarchy's power and authority was enforced to guarantee the internalization of Western culture, and its effective domination. Natives were no longer exempt from paying taxes; they paid with labor (e.g., textiles, wild cacao), further securing their conversion into faithful and industrious vassals (Ribera 1989 [1786-1794]: 207-212; Weber 2013: 164-175). Some of them resisted and even rebelled, while others made common cause with the new administrators, recreating new leadership structures based on inherited mission culture. This did not imply the abandonment of their ethnic identity and cultural traits (Block 1994).

Reformist policies sought to mobilize the native workforce, and thereby rationalize and increase the region's production and assure the desired stimulation of colonial trade and industry. Cattle herding expanded; production of crops such as cocoa, rice, manioc, tobacco, and banana increased; and manufactured goods diversified. Native production in the Spanish Amazon drew the attention of traders. In some cases, civil administrators were in charge of all transactions. In others, direct trade with outsiders was restricted to specific dates each year. Indigenous populations kept providing services to the Crown (Block 1994: 126-141; Radding 2008: 120-138). Under the Directorate rule, the growth of agriculture and the introduction of commerce were seen as the best means of "civilizing" Amazonian peoples. They could be employed in agriculture, expeditions, or provide services for settlers and provincial authorities. The director not only decided for whom they would work, and therefore what activities they would perform, but also administered payments. Additionally, they had to harvest town communal lands, with production for both local consumption and to supply cities, state employees, and the Boundary Commissions. Indigenous people worked on large coffee or sugar plantations alongside African slaves brought to the Amazon by the Grão-Pará and Maranhão trading company (Hemmig 1987: 11-17, 40-52; Melo Sampaio 2004). Furthermore, natives were inserted into smuggling networks established by merchants, clergymen, soldiers, and governors in the border areas between the different crowns (Sommer 2006; Lopes de Carvalho 2011).

The new system made Indigenous peoples more vulnerable to labor demands, expropriation of their lands, abuse by those in charge of the towns, and exploitation of the natural resources on which their subsistence depended. In the Spanish domains, the division between temporal and spiritual affairs brought tensions between state officers and the clergy, generating conflicts between them and native leaders. In Directorate villages, directors received a percentage of production as reward for their work; this encouraged physical abuse and increasing overexploitation of Indigenous labor. During the 40 years that this rule was in force, the population administered in Pará and the Amazon fell by over a third, from 30,000 in 1757 to 19,000 in 1798 (Hemming 1987: 57, 60).

All these factors contributed to the depopulation and disintegration of towns (but not all, not even the majority), increased the spread of disease, and promoted desertions (Merino and Newton 1994: 28-30). Most Indigenous peoples under the protection of mendicant orders or whose settlement had been late abandoned the missions and returned to life in the forests. Occasionally they joined communities of African slaves who had fled colonial domination. This phenomenon took place particularly, but not exclusively, north of the headwaters and middle reaches of the Amazon River. Many descendants of these populations in voluntary isolation on remote tributaries were encountered by ethnographers and missionaries in the 19th and 20th centuries, who misclassified them as "uncontacted" groups (Sommer 2019).

9.10 Indigenous resistance against conquest and colonization

From the arrival of the first conquerors until the end of the colonial period, multiple mechanisms of domination were implemented in the Amazon, to which Indigenous peoples responded with a variety of forms of resistance and rebellion. Broadly, three phases can be observed in the relationship between the conquerors and Indigenous peoples of the Amazon. The first was characterized by incursions of the latter up to the early 17th century. The second occurred between the second half of the 17th century and the first half of the 18th century, with the establishment of settlements, cities, missions, and forts, and the entry of various colonial agents, mostly merchants, including slave traders, along the rivers. The third phase started in the second half of the 18th century, during the most serious attempts to consolidate colonial power within the framework of competition between Portugal and Spain, including through Boundary Commissions and expeditions as a result of the Madrid and San Ildefonso treaties.

Although some mechanisms of domination developed during colonization seem to have disappeared, others have left explicit or indelible marks upon the present. The numerous expeditions that entered the Amazon in search of riches were characterized, according to reiterative elements in chronicles of the time, by the looting of villages in search of food and by coercion of the natives, forcing them to build boats and stay in forts or European settlements (Maurtua 1906; Carvajal [1541-1542] 2007). Appropriation of the livelihoods of Indigenous populations was accompanied by attempts to control them as a workforce.

At first, the conquerors were received with hospitality, but news of their abuses progressively spread and the initial reception on good terms became a declaration of enmity (Carvajal [1541-1542] 2007; Santos-Granero 1992). The most frequent expressions of resistance in the first phase of conquest were the abandonment and burning of villages and crops, as well as the constant harassment of expeditions. In many cases, harassment of expedition members transformed into confederate movements that involved several Indigenous peoples. At times, these movements managed to liberate large territories and expel the conquerors for decades. Among the oldest confederate rebellions, in 1541, the Quijos revolted against Francisco Pizarro's expedition with the participation of several ethnic groups from the left bank of the Coca River, who were victims of torture to obtain information about the location of the Country of Cinnamon (Santos-Granero 1992). In the same way, the expeditions of Juan Alvarez Maldonado and Gómez de Tordoya through Cusco and La Paz, respectively, and the conflicts between them, ended up inciting a confederate movement among the Araona, Toromona, Tacana, and Leco in the present-day Apolobamba region in Bolivia (Ibáñez Bonillo 2011; Lehm 2016).

As Spanish and Portuguese settlements were consolidated, colonial institutions for dominion gained a foothold. Although it is often claimed that *encomiendas*, *repartimientos*, and forced labor in the colonial *obrajes* and mines were institutions confined to the high Andes, evidence from the foothills shows that they were also present in the Amazon, although dispersed. Between 1560 and 1579, the Quijos area was the scene of two uprisings in response to abuses by *encomenderos*. The second, led by Jumandi, managed to destroy some Spanish cities such as Ávila, Archidona, and Baeza. After the defeat of the Quijos, the Jesuits used the route to establish the missions of Maynas (Uribe Taborda *et al.* 2020: 58-63; Campion Canelas 2018: 121-122; Ruiz Mantilla 1992).

In some places, usurpation of land and extraction of natural resources was accompanied by the subjugation and exploitation of Indigenous labor. Between 1579 and 1608, in a state of permanent uprising, the Shuar, Achual, and Huambisa, among other Indigenous peoples, rose up in the face of abuse by colonial agents who had forced them to labor in gold mines. Led by Quiruba or Kirub, they took the cities of Logroño de los Caballeros, Sevilla del Oro, Valladolid, Huamboya, and Zamora. The Iberians fell back, and a “frontier” was “established” which lasted well into the 20th century. The uprising had significant influence and spread to other areas of the Amazon and the foothills (Santos-Granero 1992: 215-220; Campion Canelas 2018).

The establishment of religious missions implied greater impact, since they facilitated the spread of disease. Missionaries put pressure on the cultural, religious, and governing systems of Indigenous peoples, and promoted linguistic and cultural homogenization. These actions encountered various forms of resistance; progressive and massive abandonment of the missions, open attacks or the death of missionaries and soldiers, or movements involving various groups, such as the great rebellion of the Cocama nation between 1643 and 1669, or that of the Pano groups from Ucayali in 1766 (Santos-Granero 1992: 220-226, 227-232).

In the territories controlled by the Portuguese, colonial domination was characterized by the capture and enslavement of Indigenous peoples for the production of sugar, cocoa, and other agricultural products. In 1720, Portuguese incursions through the Negro River encountered resistance, led by Ajuricaba of the Manao people, who managed to unite the different groups of that river, slowing the advance of the conquerors (Sommer, 2019).

The treaties of Madrid and San Ildefonso implied the deployment of expeditions and Boundary Commissions. These processes, which lasted several years, had a serious impact on Indigenous societies. At times, leaders and even entire Indigenous peoples had no choice but to collaborate with Spain or Portugal. Alternatively, they resisted by maintaining a permanent state of war, in which the missioners played their role (Zárate, 2014). In 1755 and even 1766, multi-ethnic articulations persisted in the Negro River region, based on wide pre-colonial networks, with complex and dynamic leadership systems, made even more complex with the incursion of agents linked to the colonial world and relationships between the internal and external policies of Indigenous peoples. In the late-18th century, colonial control of the territory did not materialize despite multiple attempts. Indigenous leadership demonstrated sophisticated political and diplomatic strategies and the maintenance of a permanent state of war. This case also highlights the approach, not always effective, of both the Spanish and Portuguese empires to incorporate Indigenous peoples into the colonial system by recognizing their authorities and granting them privileges (Melo Sampaio, 2010).

Between 1770 and 1790, the Tapajós region was the scene of attacks by the dreaded Munduruku. At first, the target of their offensives were canoes conducting Indigenous captives, followed by any colonial agent, man, woman, or native in league with the colonists. Their constant violent resistance allowed them to avoid being ruled by the colonial regime (Sommer, 2019). In the late 18th century, peace agreements were forged between the Portuguese and important factions of Karajá (1775), Kayapó do Sul (1780), Mura (1784-1787), Xavante (1788), Mbayá-Guaikurú (1791) and Mundurukú (1795) (Roller 2019: 641).

Some rebellions had messianic characteristics, combining elements of Indigenous mythology and Catholicism. These types of movements became more frequent in the late 18th century. The one led by Juan Santos Atahualpa in the central jungle of Peru stands out, as it linked different peoples, such as the Yanesha, Asháninka, and Piro, individuals or groups from the Andes such as Juan Santos of Cusquean origin, and mestizo and Afro-descendant settlers (Santos 1992: 233). After the uprising, the region was isolated from the rest of the Viceroyalty of Peru until 1847, a hundred years later, when new attempts at colonization began in the republican period. Indigenous peoples regained their autonomy and their pre-conquest ways of life, but also maintained elements brought by the Spaniards, such as cattle raising and the cultivation of fruit trees of European origin. Also, very importantly, they kept running numerous smithies to forge tools and iron artifacts (Varese 1973; Zarzar 1989; Santos-Granero 1993).

9.11 Conclusion

The European conquest and colonization of the Amazon entailed intensive transformations in the territory, especially among its ancestral peoples. The presence of the kingdoms of Spain and Portugal, but also, to a lesser extent, of France, Holland, and England, was decisive in the configuration of the region in political, administrative, jurisdictional, economic, legal, linguistic, social, and cultural terms.

From the beginning, the Amazon was viewed by Europeans as a space with inexhaustible riches ready to be extracted. This imagery, which intensely circulated in Europe, referred to fables about places and objects of gold and to myths of Greek origin, such as that of the warrior women that would end up giving the entire region its name. Colonial agents (state officials, soldiers, adventurers, clergymen, and scientists) were essential emissaries of these kingdoms for the knowledge and control of the Amazon's inhabitants and their territories.

Navigable rivers, from the Andes or the Atlantic coast, allowed European exploration, exploitation of natural resources, and the enslavememnt of Indigenous peoples. These activities further reaffirmed the territorial claims of each crown over this "new" space. Europeans settled across the Amazon. Formal institutions of colonial origin such as the *encomiendas* and the captaincies of the early 16th century later led to the erection of towns and cities of different types; some of Iberian civil and military populations, African slaves, and Indigenous slaves, and others of missionary origin with mainly native populations. These cities were footholds for expeditions of the basin beyond the great central river, in search of new Indigenous peoples, natural and mineral wealth, and territories. Rivers were the most used routes. Disputes on access to Amazonian heritage resulted in border conflicts due to imprecise, fragile, and changing treaties between the crowns. Expeditions, especially in the 18th century, increased geographical knowledge and improved regional cartography, making it possible to more precisely define those boundaries.

Domination of native populations was carried out with the power of the sword and firearms, the liturgy, and agricultural tools. The main objectives were to control people as a workforce and to ensure the productivity of the "discovered" lands. Relations were built on the roots of the "civilization/barbarism" dichotomy, founded on the presence (or absence) of certain forms of culture, both urban and agricultural. Indigenous peoples were portrayed as being in the process of "civilization" and were gathered whenever possible in urban and religious mission centers where they participated in activities associated with colonial interests. Autonomous people living in the forest were labeled "barbarians" or "savages." This classification generated a chain of "staggered disparagements" that has lasted to today and can be seen in relations between national societies and Indigenous peoples, and frequently between Indigenous peoples themselves, and have been shaping social relations and public policies since the colonial period.

The *encomienda*, mission villages, and slavery forced natives to participate in European economic activities and favored the spread of disease, with the consequence of demographic decline and extermination. Depopulation reinforced the myth of the great Amazonian emptiness, justifying its occupation by Europeans. Missionary organizations also led to the territorial and demographic fragmentation of groups as they left their traditional lands to migrate elsewhere or accepted the new social, economic, political, and labor order. The concentration of Indigenous peoples in urban centers with relatively different cultures and their contact with Europeans led to ethnogenesis processes, with the display of missionary dimensions within their cultures and diverse crossbreeding. As a result, many of them are now considered "less Indigenous" in an attempt to disregard their rights as such.

Reformist policies of the mid-18th century detached Indigenous peoples from missionary tutelage and incorporated them into the general colonial regime, subject ing them to the payment of taxes and the provision of labor, both for the colonial state and its economic agents. Since the 19th century, control of the native labor force mutated into practices such as *habilito* or *enganche*, perpetuating colonial structures. Republican rulers promoted policies to open roads and waterways, establish urban centers and, in particular, control and exploit populations and biodiversity.

Indigneous peoples responded to the different forms of colonial domination through various forms of adaptation, resistance, and revolt. Their strategies included a combination of searching for refuge in inland regions, harassment of expeditions and boats of the settlers, destruction of colonial urban centers, and the formation of confederations among different Indigenous peoples, who succeeded in overcoming their inter-ethnic conflicts to carry out unified actions. On many occasions, they managed to maintain autonomous spaces free from colonial domination for relatively long periods, in some cases up to the first half of the 20th century.

In short, the European presence in the Amazon introduced a series of ideas and practices of a colonial nature that persist to this day.

9.12 Recommendations

- Various appropriation practices of the Amazon region and its peoples have appeared since the arrival of Europeans. The transformation of these practices, at times related to layers of colonialism over long periods, must be signified and acted on through the breaking of historical racism, deterministic ideas of "civilization" or "barbarism," and violent and exploitative human relations of power. Policies for the present socio-ecological system require permanent critical approaches to prevent the reproduction of colonial myths and stereotypes.
- Avoid the continuous building of multiple "borders," e.g., between the policies of national States; between spaces and/or activities considered more or less "civilized" (for example between urban centers and more dispersed settlements in the forests and savannas); between agriculture and other activities carried out by Indigenous peoples and local populations; or between the Amazon and the Andes.
- Andean and Amazonian Indigenous peoples had permanently tense relations with colonial kingdoms, traceable in various forms of resistance. Overcoming these tensions, which have lasted until the 21st century, requires building respectful relations that address the needs of local populations and avoid the imposition of agendas from external actors that could, as in the past, generate conflict, dispossession, loss, extermination, violence, and other negative consequences.
- Several contemporary actors, like previous military explorers, missionaries, or scientists, continue to generate knowledges in and about the territory. It seems necessary to ensure that this information is used by and for the well-being of Amazonian populations, not to encourage new, violent, or improper appropriations by internal and external actors.

- More exhaustive research is required on the colonial history of the Amazon, especially during the 16th century.

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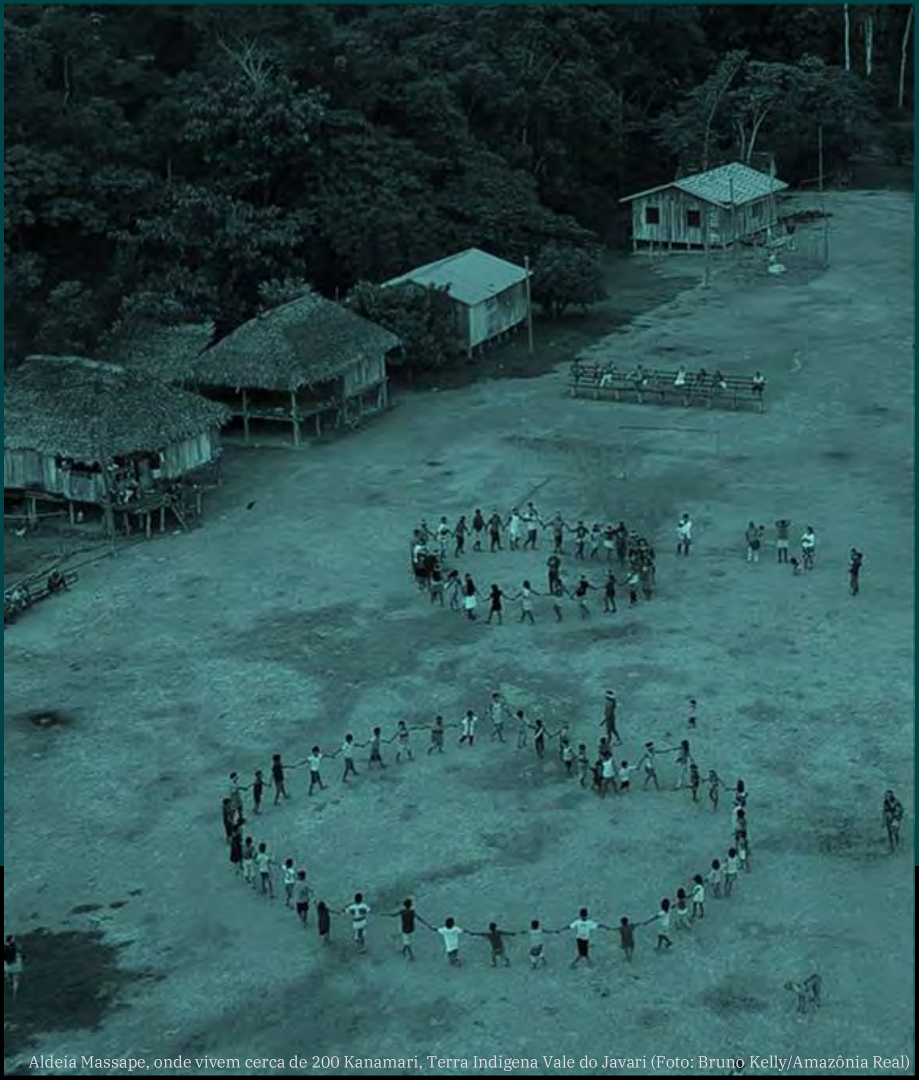
Amazon Assessment Report 2021

Chapter 10

Critical interconnections between the cultural and biological diversity of Amazonian peoples and ecosystems



Aldeia Massape, onde vivem cerca de 200 Kanamari, Terra Indigena Vale do Javari (Foto: Bruno Kelly/Amazônia Real)

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Graphical Abstract

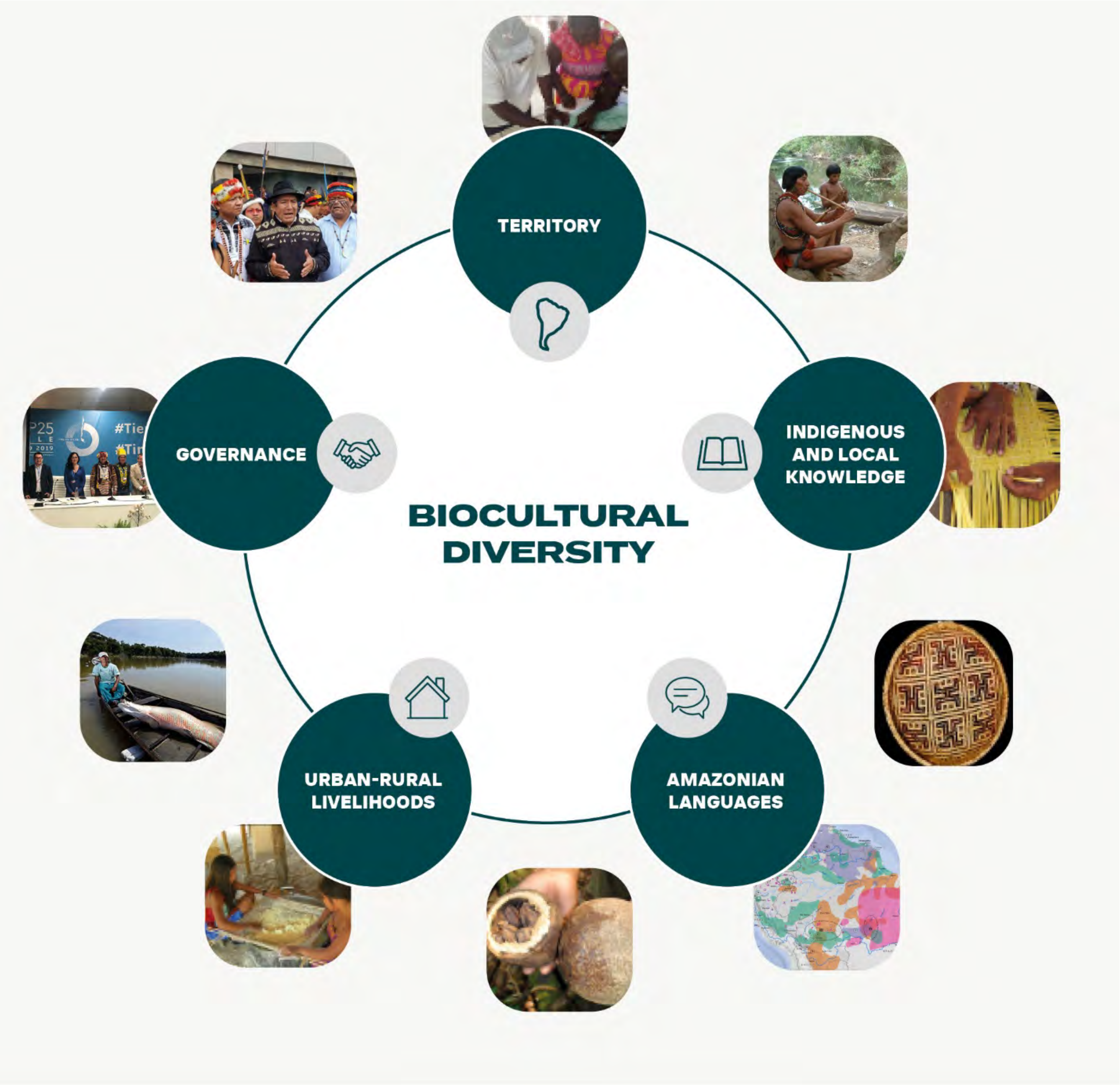

Figure 10.A This figure represents a roadmap for the different subsections included in this chapter and highlights the interconnection between biocultural diversity elements: territory, governance, languages, knowledge, and livelihoods. The concept of biocultural diversity considers the diversity of life in its human-environmental dimensions, including biological, sociocultural, and linguistic diversity. Biodiversity, cultural diversity, and linguistic diversity are interconnected and have co-evolved as social-ecological systems (Maffi 2001). These connections are present in our daily lives, in urban and rural spaces and their interlinkages, from what we eat to our livelihood styles, including our understanding and relationships with one another and with the environment around us. In this chapter, we focus more specifically on Indigenous peoples and local communities (IPLCs) across Amazonian countries, but these critical biocultural connections are manifested among all Amazonian residents.

Critical Interconnections between Cultural and Biological Diversity of Amazonian Peoples and Ecosystems

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Key Messages

- Indigenous peoples and local communities (IPLCs) play a critical role in the sustainable use and conservation of Amazonian biodiversity and ecosystems. Over 3,000 Indigenous lands and territories have been recognized across the Amazon under diverse tenure systems, which, when added to formally recognized protected areas, represent approximately 45% of the region, protecting almost half of its remaining forests (RAISG 2020; FAO 2021).
- Non-Indigenous Amazonian local communities, including small collective groups such as Afro-descendent communities (Maroons, *Quilombolas*) and extractivists of mixed descent (*mestizos, caboclos, ribeirinhos*), have been historically dispossessed and are often overlooked in scientific research, recognition of rights, and social and environmental policies.
- Recognizing Indigenous peoples' and local communities' rights to their territories and resources is fundamental for the maintenance of Amazonian forests and other terrestrial and aquatic ecosystems, carbon stocks, and biocultural diversity, including agrobiodiversity and genetic resources, as well as food security across the Amazon.
- Sophisticated environmental knowledge systems and worldviews held by IPLCs include essential resources, practices, and concepts for understanding, using, and managing the Amazon. This knowledge is critical for informing and guiding scientific research, development projects, conservation policies, and bioeconomy initiatives.
- Many Indigenous Amazonian languages are critically endangered by some of the same forces that threaten biodiversity. Just as these languages, cultures, and worldviews are in danger of extinction, so too are the knowledge systems associated with them, which are linked to and sustaining of Amazonian biodiversity.
- Women have an important role in Amazonian conservation and development, playing a critical role in the maintenance of Amazonian agrobiodiversity, food security, and sovereignty among Indigenous peoples, Afro-descendant populations, and other local communities.
- Indigenous peoples and local communities across the Amazon are stewards of diverse worldviews, values, institutions, and governance systems that are crucial not only to biodiversity conservation but also to democracy itself.

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Abstract

In this chapter, we explore important interconnections between biological and cultural diversity in the Amazon, defined as biocultural diversity. Biocultural diversity considers the diversity of life in all its dimensions, including biological, sociocultural, and linguistic aspects, which are interconnected and have co-evolved as social-ecological systems. This chapter focuses on the worldviews, knowledge systems, livelihood strategies, and governance regimes of Amazonian peoples as documented in ethnographic, ethnobiological, and human ecology studies beginning in the mid-to-late twentieth century. The focus here is on Indigenous peoples and local communities (IPLCs) across Amazonian countries and the territory of French Guiana. We synthesize important social and political processes that have led to the formal recognition of IPLCs' lands and/or territories across the Amazon, notwithstanding persistent gaps, challenges, and obstacles to the recognition, consolidation, and protection of these areas, which will be discussed in other chapters of this report. The Amazon's immense cultural diversity is manifested through approximately 300 spoken Indigenous languages, expressed in worldviews and spiritual relationships with nature. IPLCs have played a critical role in shaping, protecting, and restoring Amazonian ecosystems and biodiversity under changing contexts, despite ongoing historic processes including genocide, disease, violence, displacement, and conflicts between the conservation and development agendas. Amazonian peoples hold diverse and interconnected livelihood strategies, including agriculture and agroforestry, fisheries and aquatic management, hunting, resource gathering and extraction, and rural/urban market-based economic activities and wage-based employment in different sectors. These activities and practices are influenced to varying extents by seasonal and geographical variations, ecosystem features, cultural diversity, market forces, and public policies. We highlight the important role played by women in protecting agrobiodiversity, promoting food security and sovereignty in the Amazon. Policies aiming to conserve and use Amazonian biodiversity need to recognize the sociocultural and territorial rights of IPLCs, and be integrative of Indigenous and local knowledge, languages, worldviews, and spiritual practices.

Keywords: *Biocultural diversity; Amazonian peoples; Indigenous peoples and local communities (IPLCs); Indigenous and local knowledge (ILK); Indigenous and local cosmologies and epistemologies; livelihoods; territorial governance*

10.1. Introduction

This chapter outlines critical interconnections between sociocultural and biological diversity across the Amazon, what has been called "biocultural diversity". The concept emerged from the intersection between diverse academic disciplines and Indigenous and local knowledge systems (ILK), and recognizes that all humans are immersed in a web of interdependence between cultural, linguistic, and biological systems (Maffi and Woodley 2010). Across the globe, human cultures have co-evolved with different ecosystems through the places we live, the food we eat, the landscapes we construct, and the spiritual and political systems we advocate. In the Amazon, biocultural diversity is especially rich, as expressed through a multitude of cultural identities, worldviews, languages, knowledge systems, and livelihoods; and their associated governance regimes, technological innovations, and landscape management practices (Balée 1989, 2003; Heckenberger 2010; Salisbury and Weinstein 2014; Athayde et al. 2017a; Caballero-Serrano et al. 2019). These interlinked processes have important, but largely overlooked, implications for decision-making and policies related to biodiversity conservation and sustainable development, as discussed in other parts of this report.

For this chapter, we have adapted the definition of "Indigenous peoples and local communities" (IPLCs) as proposed by the United Nations to reflect the diversity of Amazonian peoples including those who self-identify as Indigenous, belonging to specific nations or ethnic groups, as well as Afro-descendant communities, *caboclo* or *mestizo* riverine dwellers, and forest extractivist communities such as rubber tappers, açaí collectors, palm nut gatherers, and others. Some of these peoples and communities have, through years of struggle, seen their cultural and territorial rights partially recognized by the encompassing nation states, while others have not. Therefore, in addition to the tremendous diversity of social-ecological contexts and livelihood strategies in the Amazon, there are also widely variable political and legal particulars that impinge on different peoples' sociocultural sovereignty, access to resources, and territorial rights (IWGIA 2020). This chapter focuses on the worldviews, knowledge systems, livelihood strategies, and governance regimes of Amazonian peoples as documented in ethnographic, ethnobiological, and human ecology studies beginning in the mid-to-late twentieth century. In this regard, the chapter follows up on the historical context presented in Chapters 8 and 9, while setting the stage for discussions about the contemporary Amazon in the following chapters.

The Amazon is home to approximately 47 million people living in the eight Amazonian nations of Bolivia, Brazil, Colombia, Ecuador, Guyana, Peru, Suriname, and Venezuela, plus the territory of French Guiana. Of this total, approximately 2.2 million are Indigenous people (4.6%), consisting of at least 410 distinctive ethnic groups or nations, including some 80 of whom remain in voluntary isolation (IWGIA 2020; RAISG 2020). Over 3,000 Indigenous lands and territories have been recognized across the Amazon under diverse tenure systems, which, when added to formally recognized protected areas, represent nearly 45% of the region, protecting almost half of the remaining forests (RAISG 2020; FAO 2021). More than 80% of the area occupied by Indigenous peoples in the Amazon is forested, and 35% of all Latin America's remaining intact forests are occupied by Indigenous peoples. These statistics are a clear indication of the inextricable link between cultural and biological diversity in the Amazon and highlight IPLCs as crucial partners for ongoing biodiversity conservation, as well as forest management and ecological restoration (IPBES 2019).

10.2. Colonization and territorial delimitation of the Amazon

To contextualize biocultural relationships within the complexity of post-colonial Amazonian social formations, we briefly describe the historical processes of colonization, resistance, and partial recognition of Indigenous peoples and local communities' sociocultural and territorial rights that took place during the twentieth century across Amazonian countries. A historical timeline summarizing the main moments and events that led to the current assertion of rights and territorial configurations across Amazonian countries is presented in Figure 10.1.

The very earliest European explorers of the Amazon described large villages that numbered in the thousands (Denevan 1976; Hemming 2008), and recent archaeological work has confirmed the existence of large, pre-colonial polities in some parts of the Amazon that built extensive earthworks and developed rich artistic and religious traditions (Erickson 2006; Heckenberger et al. 2008; Rostain 2008; Fausto 2020; see Chapter 8). Some Amazonian peoples engaged in long-distance trade with Andean and coastal peoples (Camino 1977; Santos-Granero 2002). European colonization resulted in enslavement, displacement, decimation from diseases, violence, and the cultural extinction of many Indigenous peoples since the sixteenth century (see Chapter 9). Complex pre-colonial political formations and artistic traditions found in the archaeological record were all but exterminated in the first hundred years of European colonization (Walker et al. 2015). Therefore, the observations made by missionaries, explorers, and researchers among Indigenous peoples do not reflect the primordial, "pre-contact" status of Amazonian political and social life (Shepard et al. 2020). Instead, the social formations and ecological adaptations of historical and contemporary Indigenous peoples of the Amazon must be understood through the lens of post-conquest genocide (Beckerman 1979).

Ensuing cycles of migration and resource exploitation in the Amazon (see Chapter 11) resulted in the

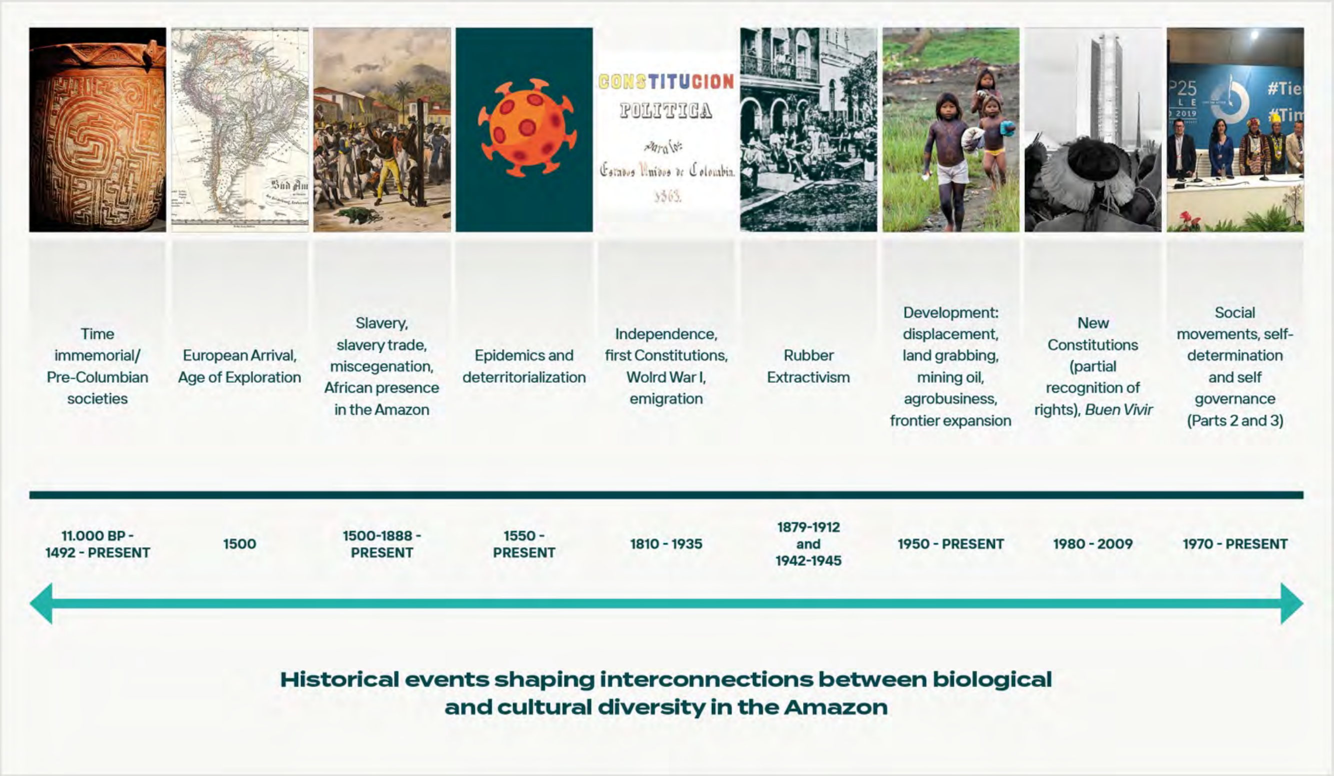

Figure 10.1 Timeline summarizing historical events affecting the sociocultural and territorial rights of IPLCs across Amazonian countries. Dates and events are approximations and do not necessarily apply to all countries or peoples, while some events and their effects are ongoing. (New Constitutions photo by Beto Ricardo/ISA; other figures under Creative Commons usage rights).

formation of diverse Amazonian identities and sociocultural groups, including peasants, riverine communities, forest-based communities, and Afro-descendant groups such as the Maroons in Suriname and French Guiana, and the *Quilombolas* in Brazil (Kambel 2006; Superti and Silva 2015; Chambouleyron and Ibáñez-Bonillo 2019). In particular, the rubber boom of the late nineteenth century resulted in a massive migration of impoverished peasants to the Amazon's interior, resulting in the enslavement, displacement, or extermination of thousands of Indigenous communities (Schmink and Wood 1992; Hecht 2010).

Throughout these historical processes, surviving Indigenous peoples, Afro-descendant communities, and/or peasants or *caboclos* constituted local communities throughout the Amazon interior and were engaged in various extractive and economic activities such as rubber tapping, hunting, fishing, mining, and plantation agriculture (Chapter 11). Extractive economies were built on a system of debt peonage that, in addition to providing cheap labor and raw materials to colonists, religious missionaries, and emerging nation states, also sought to assimilate, repress, and exterminate Indigenous cultural, linguistic, and religious diversity in the name of "civilization" and progress (Ribeiro 1962). In this sense, extractive industries and economic cycles were closely tied to the birth of nation states in Latin America and the consolidation of colonial understandings of racial and cultural superiority over Indigenous as well as enslaved African populations (Chapter 13).

Indigenous peoples and Afro-descendant populations in the Amazon have been historically judged according to racist, colonial stereotypes that viewed them as backward, inferior, primitive, and an obstacle to cultural and economic development

(Castro-Gómez 2009, 2010). Such ideologies permeated early constitutions and other laws impacting these populations in different Amazonian countries. For example, the Colombian Constitution of 1886 aimed to build a modern country "without inferior races", referring to what they called the "savages" inhabiting Amazonian forests (Castro-Gómez 2009; Marquardt 2011). Such ideologies led to the promulgation of laws promoting European immigration to several Latin American countries after World War I, in an effort to "whiten" their populations (Castro-Gómez 2009; Kabalin Campos 2018; Silva and Saldivar 2018).

The ongoing existence of isolated or "uncontacted" Indigenous peoples and historical processes of "first contact" with them have generated misconceptions in the popular imagination, reviving colonial stereotypes of people who have lived untouched in "Stone Age" conditions since time immemorial (Milanez and Shepard 2016). However, in most cases, isolated peoples belonged to larger polities who maintained networks of trade and social relations with their neighbors until recent times. Often, it was the experience of enslavement and violence during the so-called "rubber boom" at the turn of the twentieth century that forced some Indigenous peoples to choose radical social isolation from all outsiders as a survival strategy (Shepard 2016). Several Amazonian countries have developed specific policies and agencies to protect these vulnerable populations and their territories (Opas et al. 2018).

Beginning in the 1950s, and continuing through to the present, most Amazonian countries embarked on a "developmentalist" project, promoting internal colonization to hinterland areas considered demographically "empty," but in fact populated by remnant IPLCs. These policies led to the creation of internal frontiers, where land grabbing, deforestation, and resource extraction contributed to social conflicts and ideological struggles over the use and function of land (Schmink and Wood 1984). In this period, lasting until the 1980s, most Amazonian countries still viewed Indigenous peoples with a paternalistic attitude as inferior human beings who should be assimilated into the national labor force, as exemplified in the Brazilian "Indian Statute" of 1973 (Ramos 1998).

In response to oppressive labor conditions, violence, and territorial displacement produced by these processes, diverse Indigenous, Afro-descendant, and other Amazonian peoples began to mobilize, beginning around the 1970s, claiming collective rights to land, livelihood, cultural autonomy, and democratic participation (Silva and Postero 2020), while gaining attention and support from national and international social and environmental movements (Ramos 1998). The Coordination of Indigenous Organizations of the Amazon Basin (COICA) was founded in Peru in 1984, and includes member organizations in all Amazonian countries, as well as French Guiana. Amazonian IPLCs have contributed to and benefited from international initiatives such as the International Labor Organization Convention 169 of 1989, which was ratified by Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela. The right to self-determination has also been recognized in other international instruments, such as the 2007 UN Declaration on the Rights of Indigenous Peoples (UNDRIP). As a result of such national and international movements, many Amazonian countries implemented constitutional or legal reforms guaranteeing different territorial, cultural, social, and political rights to IPLCs (Figure 10.2 and Box 10.1; Cottrol and Hernandez 2001; Seider 2002; Postero 2007; Almeida 2008).

In the 1990s, the Buen Vivir (or "Living Well") philosophy emerged in Latin America as an alternative to the dominant model of capitalist development that had brought widespread poverty, inequality, and environmental destruction to the region (Gudynas and Acosta 2011; Vanhulst and Beling 2015). This philosophy is rooted in Indigenous Andean worldviews and languages (*Sumak Kawsay* in Kichwa, and *Suma Qamaña* in Aymara), focusing on the idea of collective well-being among humans, and between humans and nature. Buen Vivir principles were incorporated into the constitutions of Ecuador (2008) and Bolivia (2009).

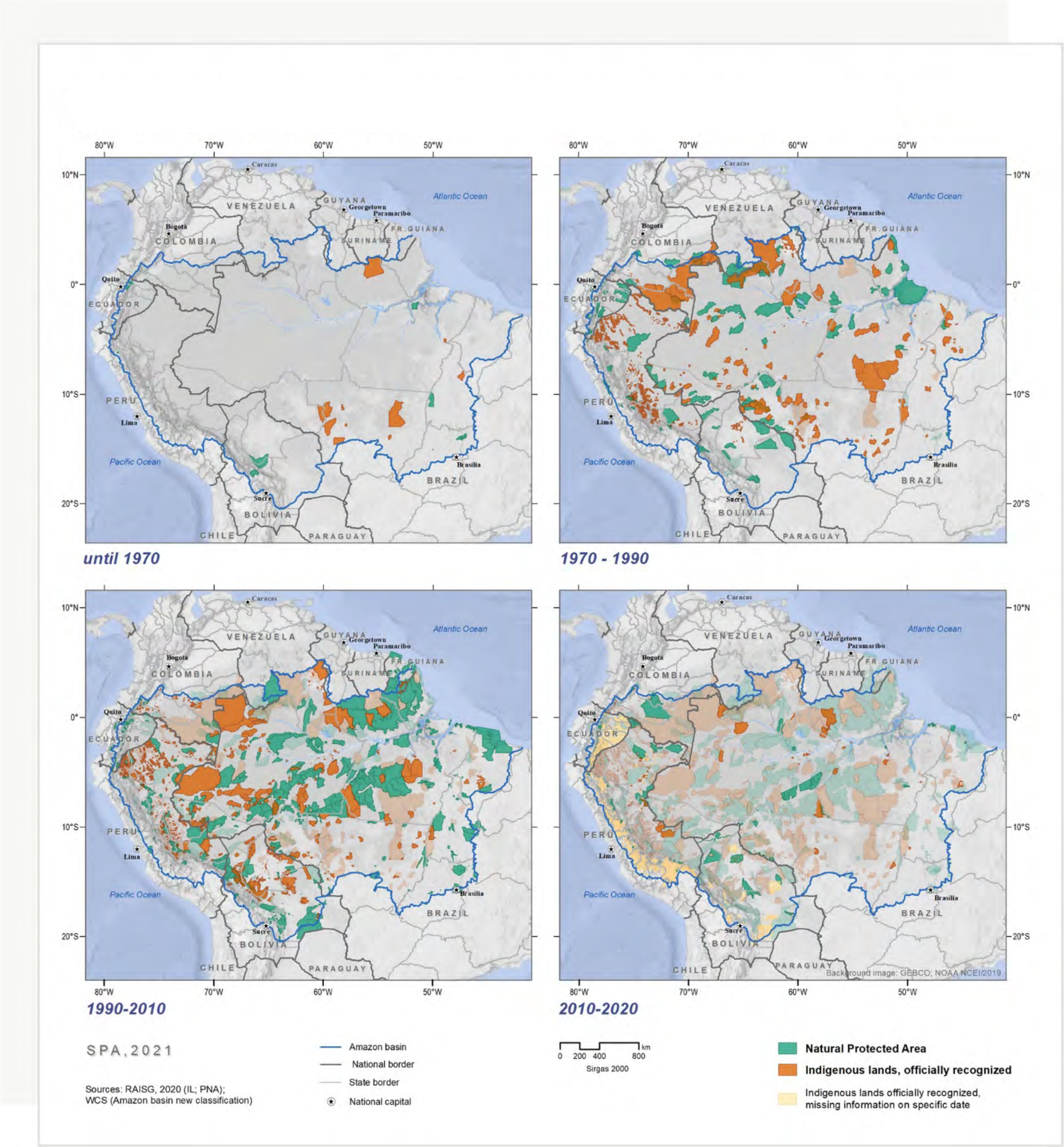

Figure 10.1 Maps showing the evolution of recognition of Indigenous territories (ITs) and protected areas (PAs) in the Amazon in different time periods. The map is limited to the Amazon drainage basin and does not include surrounding or adjacent lowlands like the Orinoco basin. Some specific country information may be missing.

Box 10.1 Paiterey Karah: The fight for the demarcation of the Sete de Setembro Indigenous Land - Cacoal - Rondônia - Brazil. By Gasodá Surui[1]

The Indigenous People Paiter, whose name means “True People'' or “Ourselves”, also known as the Rondônia Suruí, live at the Paiterey Karah, which in the Tupi Mondé language means “the land of the Paiterey.” This territory is known as Sete de Setembro Indigenous Land, a name given by the National Indian Foundation (FUNAI) as a reference to the first contact of the group with non-Indigenous peoples, which happened on September 7, 1969.

The Paiter speak a language of the Mondé family in the Tupi stock and are formed by four clan groups that make up our sociocultural life: *Gãmeb* (black wasp), *Gapgir* (yellow wasp), *Kaban* (*mirindiba* fruit), and *Makor* (*taboca* bamboo). The population in 2001 was approximately 1,500 people distributed in 28 villages established across the territory, with the objective of caring for and protecting the land against possible attacks and invasions by illegal loggers, miners, hunters, and fishers.

According to the Paiterey, the original territory, before the contact with the non-Indigenous society, extended to Cuiabá, and the current borders were nonexistent. After the arrival of non-Indigenous people, Paiter lands were invaded and the forests were destroyed. Then, the government arrived, opening the BR364 road, which resembled an enormous snake that opened up the forest, swallowing our people, diminishing our land, expelling the Paiterey, and leaving everything to the invaders.

Through intergenerational communication, the Paiter still remember the time when they ran away from their original territory in the nineteenth century, fleeing from the persecution of whites. During the escape, conflicts occurred with other Indigenous and non-Indigenous groups. From the end of the nineteenth century to the 1920s, with the exploitation of rubber, the construction of the Madeira–Mamoré railway, and the installation of telegraph lines by Rondon, the migratory flow to Rondônia increased, and its effects were felt on the Indigenous populations in the region, causing many struggles and deaths.

The physical demarcation of the Surui land happened in 1976 after significant pressure on the Brazilian government from Paiter leaders and FUNAI, involving several trips to Brasilia to discuss the matter. The homologation happened via decree 88.867 of October 17, 1983. Currently, the Sete de Setembro Indigenous Land occupies an area of 248,147 ha, located in the States of Rondônia and Mato Grosso. This is a space where the Paiter preserve their values, beliefs, and customs, and where historical processes and social relations develop. The reduction to the territory excluded important sites for Indigenous rituals, such as the Pimenta Bueno region, near the limit of Cacoal, where a *tucumanzal* (*Astrocaryum* palm stand) was located, a fundamental material for handicrafts used as body adornments during the gift exchange of the *Iway* and *Metare*, at the celebration of *Mapimaih*.

[1] Indigenous leader of the Paiter people, also known as Rondônia Surui. Graduated in Tourism from the Centro Universitário São Lucas in Porto Velho, Rondônia. Master in Geography and Ph.D. student in Geography at the Federal University of Rondônia. Creator and founder of the Paiter *Wagôh Pakob* Indigenous Cultural Center, "Force of Nature", a Paiter Indigenous initiative created in November 2016 to defend and guarantee the territory, as well as the culture and traditional knowledge of the Paiter Surui people of Aldeia Paiter. Researcher in the Geographic, Nature and Human Territoriality Research Group at the Federal University of Rondônia.

Despite these political advances and their potential contribution to the conservation of biocultural diversity, many challenges remain to the operationalization of IPLCs concepts and rights in the Amazon (Vanhulst and Beling 2015). In Venezuela and Bolivia, for example, legal land rights are granted to only a small proportion of territorial claims. In Brazil, even though approximately 21% of the Amazon region has been demarcated as Indigenous lands, agribusiness, logging, and mining interests have lobbied to undermine these established protections, leading to a new wave of conflict, rights violations, invasions, illegal deforestation, and violence against Indigenous peoples, Afro-descendant populations, and other local communities (RAISG 2020; see following Chapters). In response, Indigenous, Afro-descendant, and other Amazonian communities have recently joined together to fight for their common cause, with a striking emergence of women-led coalitions and collectives (Giacomini 2017; Mello and Schmink 2017).

10.3. Cosmologies, worldviews, and knowledge systems: Implications for natural resource management

Among Amazonian Indigenous peoples and local communities, sociocultural, political, and economic organization is mediated by specific ways through which people view and interact with the world and, more broadly, with the cosmos. These cosmologies and worldviews are differentiated within and across cultural groups and have a strong influence on people's perceptions and interactions with ecosystems and biodiversity (Hill 1988; Reichel 1999; Seeger 2004).

In contrast to European colonial societies, Amazonian Indigenous peoples do not view the forests that surround them as separate, "natural" realms full of objectified resources to be dominated and exploited by humans. Instead, they look at the diverse animals, plants, and other entities as sentient beings with their own social lives and subjective points of view (Costa and Fausto 2010; Rival 2012). In this sense, Amazonian shamans are more than healers; they are responsible for communicating and negotiating with the multitude of other beings that populate the cosmos to protect human societies (Descola 1994; Carneiro da Cunha 1998; Viveiros de Castro 1998; Shepard 2004; Athayde et al. 2016). In his autobiography, The Falling Sky, Yanomami shaman Davi Kopenawa (Kopenawa and Albert 2014: 116-118) enumerates predatory illnesses and shamanic helper spirits, the xapiri, as an encyclopedic list of biological species:

> "When they encounter us in the forest, the *në wäri* evil beings consider us game. They see us as spider monkeys and our children as parrots. It is true! This is the name they give us! We could never survive without the protection of the *xapiri*. ... Many *xapiri* are good at following evil beings' trails, including the hunting dogs and the peccary spirits, who sniff their tracks. ...
>
> The wasp spirits arrow them, the spirits of the *witiwitima namo kite* lacerate them with their sharp blades, and the coati spirits knock them out with their clubs. ... Those of the *wari mahi* tree thrash them. With their skulls split open and their bodies covered in wounds, the stunned evil beings eventually stumble. Then the *xapiri* can force them to let go of their prey and give up the fight."

Amazonian peoples view the cosmos as a kind of ecosystem (Reichel-Dolmatoff 1976; Århem 1996), and predation is a fundamental metaphor that structures the multi-faceted relationships between humans, animals, and the spirit world (Fausto 2007). Just as humans hunt and kill animals for food, certain dangerous animals, demons, and other predatory spirits look upon humans as prey. This relational understanding of Indigenous Amazonian cosmology has been referred to as "animism" (Descola 1994) or "perspectivism" (Viveiros de Castro 1996; Lima 1999), rife with transformations and exchanges that cross-cut species boundaries and defy Western dichotomies such as nature/culture, body/mind, and matter/spirit (Daly and Shepard 2019). An important aspect of Indigenous and local knowledge (ILK) is that perceptions and relationships differ between age groups, gender, and roles played in the community (Reichel 1999; Howard 2003; Athayde et al. 2017a; Athayde and Silva-Lugo 2018).

Just as Indigenous peoples' concepts about human–animal relationships challenge Western concepts about taxonomy and ontology, they also defy capitalistic notions about resource extraction and management. For example, in opposition to Adam Smith's notion of market forces governing Western economic affairs, Kopenawa (Kopenawa and Albert 2014: 149) describes the concept *në rope*, which is translated as "value of growth," a kind of "invisible hand" regulating Yanomami economy, ecology, and spirituality:

> "The value of growth remains abundant in the forest and if our gardens take the value of hunger, our shamans drink the *yãkoana* [psychoactive snuff] to bring it back home. ... When the forest's richness runs away, the game becomes skinny and scarce, for this richness is what makes the game prosper. ...This is why the shamans also bring down the image of the game's fat with that of the forest's fertility."

Amazonian farming and forest management systems are characterized by an extraordinary diversity of domesticated, semi-domesticated, and wild plants, with cyclic alternation between phases of cultivation, abandonment, and recovery (Rival 2012; Carneiro da Cunha 2017). For many Indigenous peoples, these cyclic movements are tied to special rituals and ceremonies (including songs and special body preparations) that ensure the maintenance of customary laws that regulate interactions between the physical and the spiritual worlds (Seeger, 2004). Diversity is a fundamental theme in all aspects of Amazonian livelihoods, including farming, hunting, gathering, fishing, and weaving, as well as myth, ritual, and shamanism (Shepard 1999; Emperaire and Eloy 2008; Heckler and Zent 2008; Athayde et al. 2017a,b).

Complex webs of human–nature relationships manifested in the daily lives of Amazonian IPLCs are connected to specific ILK domains, including artistic expressions such as music, weaving, body painting, pottery, and material culture in general. Among the Kawaiwete (also known as Kaiabi) of the Brazilian Amazon, highly-valued baskets woven by men are considered living entities and carry a symbolic language that connects them to ancestors and collective memory. A basket can be, at the same time, a living being, a ritualistic object, and a recipient used by women to spin cotton (Athayde et al. 2017b; Figure 10.3).

The traditional pharmacopeia of Amazonian peoples includes plant remedies for common conditions such as diarrhea, intestinal worms, leishmaniasis, and snake bites, as well as medicines to improve a man's aim when hunting, a woman's dexterity at creating delicate handicrafts, the productivity of a garden, or a person's singing abilities (Shepard 2004; Kujawska et al. 2020). In this sense, the connections between health, society, and the environment are manifold and multi-faceted, embracing physical and spiritual well-being as well as productive social, ecological, and agricultural interactions.

Indigenous peoples' worldviews and values contrast sharply with the norms, scientific practices, and governance institutions of settler-colonist nation states. For instance, Indigenous notions of "ownership" and "mastery" highlight the subjectivity, agency, and reciprocity in relations with diverse non-human beings, in sharp contrast to objectifying Western notions about property and resource use (Fausto 2008). Among local riverine communities, connections with the Amazonian pink dolphin (*Inia geoffrensis*) can take many forms. These dolphins appear in the local imagination as enchanted beings that can appear as humans and have sexual relations with women. In other circumstances, connections with this species can include partnerships or mutual hostility, invoking a reciprocal affective tie that transcends the human-animal divide (Arregui 2019).

In a recent review, Fernández-Llamazares and Virtanen (2020) examine the widespread notion of "game animal masters" among diverse Amazonian Indigenous peoples. They discuss the overlooked potential of this Indigenous notion to contribute to biodiversity conservation. In Peru, for example, the Matsigenka people say that invisible guardian spirits of the forest, the Saangariite ('invisible ones'), who raise game animals as their pets, may punish careless or excessive hunters by hiding their animals from them (Shepard 2002). The notion of panema among non-Indigenous hunters of the Brazilian Amazon also involves reciprocity with forest spirits and punishment for excessive or "perverse" hunting (Vieira et al. 2017).

The arrival of global capital markets to the Amazonian hinterlands throughout the twentieth century and the introduction of Western technologies such as shotguns, haul nets, metal tools, chainsaws, and gasoline engines, has transformed Indigenous peoples' impacts on Amazonian forests (Alvard 1995; Souza-Mazurek et al. 2000; Shepard et al. 2012). Indigenous and other forest peoples participated in market activities that reduced animal populations to the point of local extinction in some regions in the mid-twentieth century (Antunes et al. 2016). Yet, while some populations have recovered from commercial hunting, Indigenous understandings of this process may rely on cosmological and shamanic, as much as material, perceptions about the restoration of human–animal relationships (Pimenta et al. 2018).

10.4. Languages and biocultural conservation

In the Amazon, Indigenous peoples' worldviews, understanding, and interconnections with nature and biodiversity are encoded and expressed in approximately 300 to 350 Amazonian languages

Figure 10.2 Biocultural interactions expressed through basketry and textile production among men and women from the Kawaiwete (also known as Kaiabi) Indigenous people of the Brazilian Amazon. Graphic designs carry special meanings tied to Kawaiwete cosmology and spirituality (Athayde et al. 2017b). A. Wisio Kaiabi spinning cotton. B. More Kaiabi weaving a sling used for carrying babies; C. Men weaving a basket made of *tucumã* palm (*Astrocaryum aculeatum*). D. Kawintai'i Kaiabi (*in memoriam*) painting a designed basket. E. Designed basket showing the *Kururu'i* (small frog) graphic design. Photos by Simone Athayde, Xingu Indigenous Territory, Brazilian Amazon.

(Aikhenvald 2012). This is all that remain of a much bigger number of languages, after five centuries of European colonization (Voort 2019). Approximately 75% of Amazonian language diversity has been lost forever, without substantial documentation (Palosaari and Campbell 2011). The consequences of language loss are severe for the social and cultural fabric of Indigenous communities, for academic research, and for humanity as a whole. Each language represents an irreplaceable cultural heritage of specialized knowledge, art, and ways to conceptualize and understand the world, that are preserved in — and transmitted by — its linguistic categories and structures (Dorian 1989; Krauss 1992; Wurm 2001; Harrison, 2007; Moseley 2007, 2010; Evans 2010; Austin and Sallabank 2011).

As observed in Chapter 12, the Amazon region harbors exceptional Indigenous language diversity. Its languages are classified into approximately 25 different families (Crevels 2012). Furthermore, it has a world record of approximately 20 linguistic isolates that are not genealogically related to any other known languages (Crevels 2012; Seifart and Hammarström 2018). As Adelaar (1991:45) observes, this represents “unsurpassed genetic variety”.

Most Amazonian languages are seriously threatened by extinction. Although population numbers are rising, speaker numbers are dwindling due to a tendency to shift to national languages, abandoning Indigenous languages (Crevels 2002; Grinevald 1998). Language shift is usually motivated by migration or perceived economic advantages in a dominant monolingual society (Harbert 2011; Thomason 2015). So far, only a few inventories reliably map the actual socio-linguistic situation of Amazonian languages (Sichra 2009; Galucio et al. 2018). Unfortunately, just like biological species, languages are becoming extinct before we even know what is lost.

Local languages may convey ILK and linguistic structures intricately linked to biodiversity. Ethnoecological studies among several Amazonian peoples have revealed a detailed vocabulary for classifying forest habitat types according to geomorphology, hydrology, soil types, and salient indicator species (Parker et al. 1983; Fleck and Harder 2000; Abraão et al. 2010). In some cases, Indigenous habitat classification is comparable to, or even more sophisticated than, contemporary scientific classification systems and can be applied to “ground truth” satellite imagery or streamline biodiversity inventories (Shepard et al. 2004; Abraão et al. 2008). Shepard (1997) and Zent (2009) have documented bioculturally relevant systems of noun classification in the languages of the Matsigenka people of Peru and the Uwojtüja (Piaroa) of Venezuela, respectively. Numeral classifiers in Matsigenka refer in their most basic sense to plants or plant parts, but can be applied in derived forms to create culturally relevant analogies between plants, animals, and material culture (Shepard 1997). Likewise, among the Piaroa, of more than 100 commonly used noun classifiers, at least 75 are used to categorize and distinguish between different botanical life forms, plant parts, growth habits, and ecological associations. This linguistically encoded system is comparable to the scientific botanist’s taxonomic key, as it facilitates their ability to recognize and classify several hundred plant taxa. These and other examples provide specific instances of how the maintenance of folk botanical knowledge is directly dependent upon language preservation (Zent 2009).

Language loss is likewise connected with environmental destruction and the extinction of biological species, especially in the Amazon. In the past decades, the interdependence of linguistic and biological diversity has become increasingly obvious (Maffi 2001; Loh and Harmon 2005; Gorenflo et al. 2012). Those regions of the world with the highest species diversity also contain the highest linguistic diversity. The similarity between evolutionary biological speciation and language genesis was noted by Charles Darwin (1871).

In the 1988 Declaration of Belém, conservation biologists, ethnobiologists, and anthropologists acknowledged the existence of an ‘inextricable link’ between biological and cultural diversity. Seminal articles (Harmon 1996; Golan *et al*. 2019) helped identify biolinguistic diversity hotspots in the Amazon Basin, Central Africa, and Indo–Malaysia/Melanesia (Maffi 2001; Loh and Harmon 2005, 2014). Approximately 70% of the world's languages are spoken on approximately 24% of the earth's terrestrial surface, comprising regions of high biodiversity (Gorenflo et al. 2012). Furthermore, as Harmon and Loh (2018) indicate, "analysis of the conservation status of languages indicates that they are more threatened overall than mammals, birds, or reptiles, and as severe a state as amphibians."

Language extinction due to shifts triggered globally by urbanization, migration, and other factors is relatable to environmental destruction and habitat loss in the Amazon. As recent satellite images

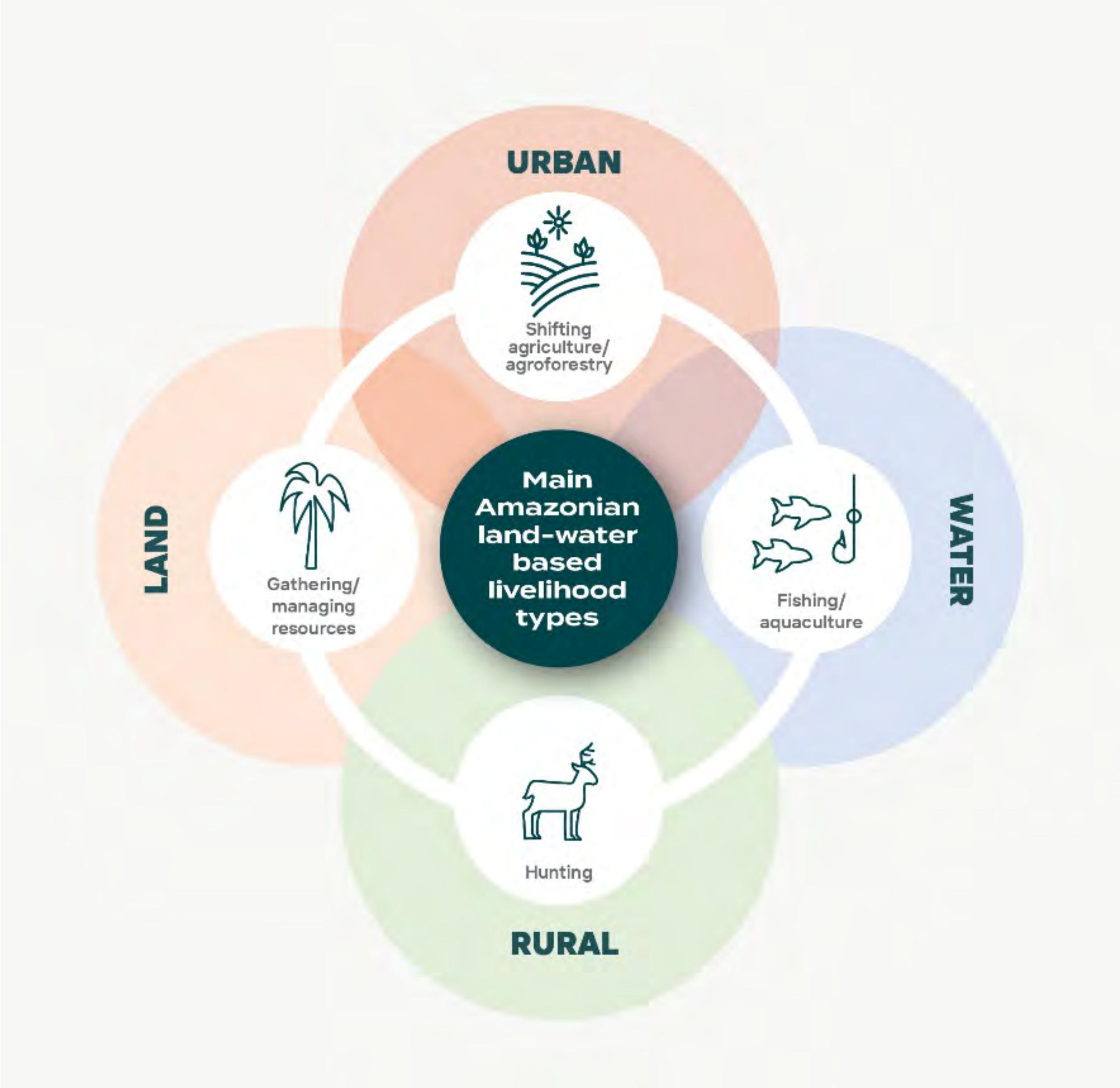

Figure 10.3 Multi-sited rural–urban livelihood strategies of Indigenous peoples and local communities in the Amazon.

show, those parts of the Amazon where Indigenous peoples live and whose languages survive also tend to be those parts that are still green. Frainer et al. (2020) highlight the fact that national and international policies have approached cultural, linguistic, and biological diversity separately, whereas these “diversities” have co-evolved and shaped the world as we know it. Therefore, the integration of ILK and languages in biodiversity assessments, management, and policies is crucial.

10.5. Biocultural diversity, lands, and livelihoods

As seen in previous sections, scientific studies of ILK systems and their corresponding imprint on the landscape have revealed different entanglements of cultural and natural diversity that were first described by historical ecologists (Posey 1985; Balée 1989, 2003, 2013). With the recognition and delimitation of Indigenous lands that took place beginning in the 1970s through the 1990s in many Amazonian countries, and the more recent (partial) recognition of collective land rights for Afro-descendant populations in some countries (*Quilombolas*, Maroons), the livelihoods of IPLCs have been increasingly shaped by national and international policies; by governmental, non-governmental, and scientific institutions; and by market forces and rural-urban networks (Piñedo-Vasquez et al. 2008; Figure 10.4; Chapter 14).

The concept of biocultural landscape and heritage recognizes the reciprocal relationships between IPLCs and forests, rivers, and other Amazonian ecosystems since time immemorial to the present (Cross-Chapter 31.A). For example, the Jodï people of Venezuela do not inhabit the forest in a passive way, but are active agents in constantly recreating a living forest through several management practices encoded in specific linguistic concepts and spiritual connections (Box 10.2, Figure 10.5).

Like Indigenous peoples, Afro-descendant and other Amazonian communities engage in multi-sited rural-urban livelihoods that are finely tuned to diverse ecosystems as well as seasonal fluctuation in river levels, especially in the flooded *varzea* forests along the main channel of the Amazon and its larger tributaries (Adams et al. 2009, see Chapter 14). Referred to variably as *caboclos, mestizos*, peasants, or “riverine” dwellers (*ribeirinhos*), these populations have intensively participated in regional, national, and global markets through extraction, processing, and commercialization of forest resources (Fraser et al. 2018). Since the colonization of the Amazon associated with different economic cycles in the nineteenth and twentieth centuries, IPLCs’ livelihoods have been connected to global consumption and technological developments, as well as to national and regional fluctuations in demand for wage labor (Fraser et al. 2018; Chapters 11 and 14). Geographer Bertha Becker (in memoriam) refers to the Amazon as an “urbanized forest,” describing urbanization processes that began in the 1980s triggered by the construction of railroads, highways, ports, and the vehiculation of urban society (Becker 2005). This understanding has direct relevance to the design of integrated policies that consider the interconnected nature of cultural and biological diversity in the Amazon.

10.5.1. Amazonian agriculture and agroforestry

Traditional agricultural systems of the Amazon include a multiplicity of cultivated and managed plants and involve complex strategies of landscape management and integration with other livelihood activities such as hunting, fishing, and extractivism, as well as with urban markets (Denevan et al 1988; Emperaire and Eloy 2008; Porro et al. 2012; Clement 2019). The Amazon is a center of genetic diversity for diverse crops such as cassava, peanuts, maize, sweet potato, yam, chili peppers, and cacao (Figure 10.6; Clement et al. 2015; Zent and Zent 2012). Women often play an important role in food security and sovereignty through their cultivation, exchange, management, and conservation of crops (Silva 2004; Emperaire and Eloy 2014).

Cassava or manioc (*Manihot esculenta*) is the primary staple crop for many contemporary Indigenous peoples and peasants and other local communities of the Amazon (Boster 1984; Salick *et al.* 1997;

Figure 10.4 Juae and a younger kinsman (*jluwëna*) playing a flute known as *ja̲ni jtawibo* on the banks of the Kayamá river during a hunting expedition. Credits: Yheicar Bernal, Stanford Zent, and Eglée Zent, photo taken in 2005 in the Kayamá river, Estado Bolívar, República Bolivariana de Venezuela.

Clement et al. 2010; Table 1). Indigenous peoples cultivate hundreds of land races and varieties of manioc (Frechione 1982; Heckler and Zent 2008; Emperaire and Eloy 2008), most of which are divided among two major types, "bitter" manioc, containing toxic levels of cyanide and requiring detoxification before consumption, and "sweet" manioc, edible after simple boiling. These two principal types correspond to two main culture areas in the historical and contemporary Amazon, with bitter manioc cultivation found principally along the courses of the major Amazonian rivers in the central and eastern Amazon and coastal areas, and sweet manioc cultivation predominant along tributary and headwater rivers, especially in the western Amazon (McKey and Beckerman 1993; Clement et al. 2010).

Bitter manioc cultivation in the northwestern Amazon is associated with tremendous agrobiodiversity of manioc cultivars (Emperaire and Eloy 2008), as well as cultural innovations in the processing and removal of lethally toxic cyanogenic glucosides, notably the woven tipiti manioc press and a wide range of specialized basketry (Figure 10.7; Ribeiro 1980; Dufour 2007). Processes associated with bitter manioc cultivation are deeply integrated into social, symbolic, and cosmological systems (Hugh-Jones 1980; Chernela 1993).

Like other documented cases of agricultural systems of Indigenous peoples in the western Amazon (Boster 1984; Johnson 2003), the polycultural swidden agricultural systems of the Kichwa Indigenous people in Ecuador contain a great diversity of cultivated and managed food, medicinal, and ritual species (Coq-Huelva et al. 2017). Known locally as chakras, these systems reflect Kichwa worldviews and values as expressed in the philosophy of *Sumak Kawsay* or "Living Well," which reinforces collective management and reciprocal relationships between humans and non-human beings (Acosta 2016

Box 10.2 The Jodï people: Livelihood strategies, biocultural diversity, and spirituality in Venezuela

The Jodï Indigenous people possess a rich knowledge of primary forest species and their uses, including more than 220 edible species, 180 medicinal plants, 190 species with other technological uses, and 550 species known to be eaten by wildlife (upon which people depend for food) (Zent 1999).

A close examination of Jodï subsistence practices reveals that they do not merely exploit the forests they inhabit but also create them to some extent. Specific manipulative techniques related to their foraging and trekking habits were shown to have a considerable effect on forest composition and the distribution of species. The harvest of wild fruits, for example, often involves the felling of older trees and cutting of branches, thus opening up light gaps. At the same time, people eat fruits and deposit seeds on the spot. Another practice is the small-scale application of fire to grassy spots and fallen tree crowns. It is common to find stands of fire-resistant, economically-important palms and heliconias colonizing these areas. Seje (*Oenocarpus bacaba*) and maripa (*Attalea maripa*) palms are often felled for fruit and to create a suitable growing environment for palm larvae, a favorite food.

Besides creating light gaps, the Jodï also make use of natural tree fall clearings by transplanting useful species in them. Such managed spaces are often found close to trails at great distances from main settlements and provide future resource caches during trekking expeditions. Taken together, these environment-modifying activities make for a very patchy, diversified landscape. This case study corroborates not only the anthropogenic nature of Amazonian forests, but also shows that native foragers continue to make substantial contributions to this process (Zent and Zent 2004).

The most impressive and prolific linkage between the Jodï and biodiversity lies in their worldviews, ritual practices, and the notion of personhood. The notion of what constitutes the soul or spiritual being(s) of a person (their *jnamodi*) is literally wrapped up in the diversity of living organisms around them and with whom they have contact throughout their lives. When a baby is born, the father must go out into the forest and collect an organic bundle consisting of the tiny pieces or remains of many different species of trees, vines, herbs, mushrooms, insects, mammals, birds, dirt, and other natural substances. In some reported cases, the bundle contains more than 100 different species. He then comes back and bathes the infant with the macerated bundle to form its spiritual self, called *jnamodï*. The *jnamodï* of a person acts as their intangible intermediary in their dealings with the forest and its various living entities. The fact that one shares a spiritual kinship with those entities facilitates prosperous and sustainable interactions, such as hunting success, bountiful harvests, and immunity from pathogenic contagion (Figure 10.5). Therefore, according to Jodï cosmology, every person spiritually consists of a diversity of different species. People are not only dependent on the biodiverse forest, they are part of it (Zent et al. 2019).

Chapter 14). Chakras are especially associated with women's activities such as planting and tending cassava, potatoes, and other root crops, as well as preparing fermented manioc beer (Whitten 1978). The Kichwa chakra system has provided strategic and diverse food resources to confront the rapidly changing contemporary context (Coq-Huelva et al. 2017).

Amazonian Afro-descendant groups and peasants or *caboclos* have also developed sophisticated agricultural and agroforestry systems, contributing to the rich agrobiodiversity represented in the region. A study of the Aluku Maroons (Afro-descendant group) of French Guiana documented 38 cultivated crops, with 156 varieties (Fleury 2016). Further research for the documentation and "in-situ" conservation of these varieties should be a priority, respecting IPLCs intellectual property rights over these important genetic resources (Santilli 2012).

Agroforestry systems are an integral part of swidden cultivation or slash-and-burn agriculture as practiced by contemporary Amazonian peoples (Hauser and Norgrove 2013). Hundreds of species and varieties are cultivated in swidden-fallow agroforestry systems, with staple cultigens such as manioc and maize (*Zea mays*) raised alongside, or in succession, with managed agroforestry species such as peach palm (*Bactris gasipaes*), cacao (*Theobroma cacao*), açai palm (*Euterpe oleracea*), babaçu palm (*Attalea speciosa*), and Brazil nut (*Bertholletia excelsa*), among many others (Pinton and Emperaire 1992; Porro et al. 2012; Chapter 11). Owing to long fallow periods, Indigenous agroforestry systems imitate the forest in terms of their structure and diversity (Posey, 1985; Denevan et al. 1988), and swidden fallows enriched with dozens of protected, managed, or semi-domesticated plant species can be understood as intermediates between agricultural zones and forest ecosystems (Alcorn, 1989; Cardoso 2010; Cardoso et al. 2010).

Rooted in the agricultural practices of Indigenous peoples, the field of agroecology emerged in the 1970s-1980s as a response to the socio-environmental damage inflicted by the Green Revolution (Altieri 1996; Holt-Giménez and Altieri 2013).

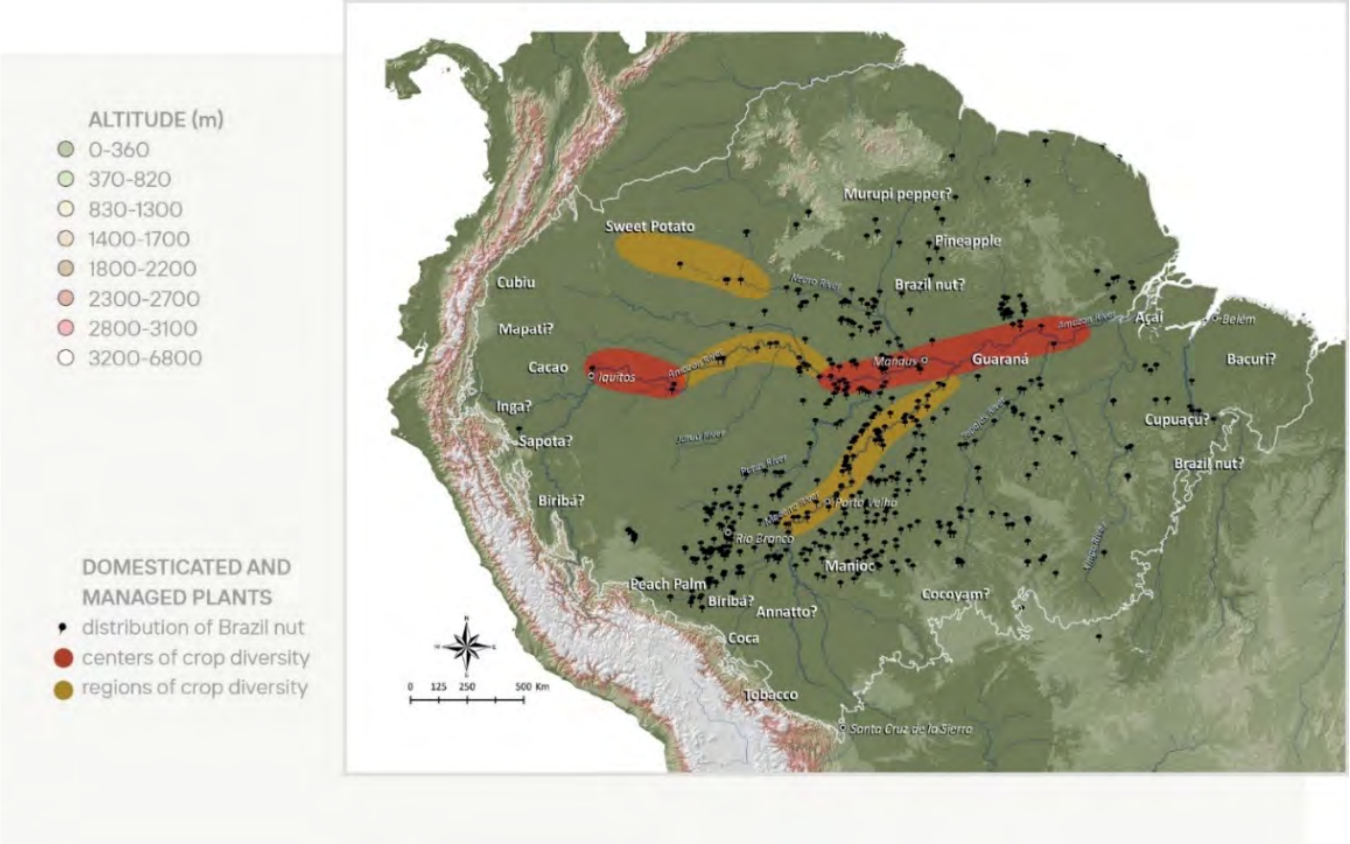

Figure 10.5 Plant and crop management and domestication in the Amazon. The names of species identify the known or potential origins of domestication of 20 native Amazonian crop species. The centers and regions of crop genetic diversity include significant or moderate concentrations of crop genetic resources. Source: Clement et al. (2015).

Table 10.1 Varietal diversity of Manioc (*Manihot esculenta*) in the Amazon. Source: Cunha and Lima (2016). Details about the sources for the information provided can be found in the original article.

Indigenous peoples traditional local communities	*Area*	*Sweet*	*Bitter*	*Sweet + Bitter*	*Source*
Amuesha (Aruak)	*Peru*			*204*	*Salick et al. 1997*
Wanana, Tukano, Arapaso	*Middle Uaupés, AM, Brasil*			*137*	*Chernela 1986*
Pluri-ethnic communities: Barcelos	*Middle Rio Negro*			*120*	*Corbellini 2004*
Piaroa (Piaroa-Saliban)	*Cuao and Manapiare (Orinoco basin), Venezuela*			*113*	*Heckler and Zent 2008*
Pluri-ethnic communities: Santa Isabel	*Upper-Middle Rio Negro, AM, Brazil*			*106*	*Emperaire, Eloy 2014.*
Tukano (Uaupes)	*Uaupés, AM, Brazil*			*100*	*Emperaire 2002*
Aguaruna (Jivaro)	*North Central Peru*			*100*	*Boster 1984*
Huambisa (Jivaro)	*Peru*			*100*	*Boster 1983*
Tatuyo (Tukano)	*Uaupés, AM, Brazil*			*100*	*Dufour 1993*
Wajãpi (Tupi-Guarani)	*Amapá, Brazil*	*94*	*3*	*97*	*Oliveira 2006*
Aluku (quilombola)	*French Guiana*			*90*	*Fleury 2016*
Makushi (Karib) e Wapishana (Aruak)	*Roraima, Brazil Guyana, Venezuela*			*76,77*	*Elias et al. 2000* *Daly 2016*
Cubeo, Piratapuia e Tukano (Tukano), Tikuna (Tikuna) e Sateré-Mawé (Mawé)	*Cuieiras river, Lower Rio Negro, AM, Brazil*	*65*	*5*	*70*	*Cardoso 2008*
Wayana (Karib)	*French Guiana*			*65*	*Fleury 2016*
Pluri-ethnic communities	*Middle Rio Negro, AM, Brazil*			*64*	*Emperaire et al. 1998*
Bare (Aruak)	*Upper Rio Negro, AM, Brazil*			*60*	*Emperaire 2002*
Local communities Mamirauá and Amanã	*Middle Solimões, AM, Brazil*			*54*	*Lima et al. 2012*
Kayapo-Mebêngôkre (Gê)	*Pará, Brazil*			*46*	*Robert et al. 2012*
Kuikuro (Karib)	*Upper Xingu, Mato Grosso, Brazil*			*36-46*	*Carneiro 1983; Heckenberger 1998; Smith and Fausto 2016*
Pataxó (Macro-Gê)	*Bahia, Brazik*			*34*	*Arruda Campos 2016*
Paumari (Arawa)	*Purus, AM, Brazil*			*14-30*	*Prance et al. 1977; FUNAI/PPTAL/GTZ 2008*
Krahô (Timbira-Gê)	*Tocantins, Brazil*	*9*	*12*	*21*	*Dias et al. 2007–2014; Morim de Lima 2016*
Canela-Ramkokamekra (Timbira-Gê)	*Maranhão, Brazil*	*7*	*9*	*16*	*Miller 2015*
Kaiabi (Tupi-Guarani)	*Mato Grosso, Brazil*	*9*	*6*	*15*	*Silva 2009*
Enawenê-Nawê (Aruak)	*Mato Grosso, Brazil*	*14*	*1*	*15*	*Santos 2001*

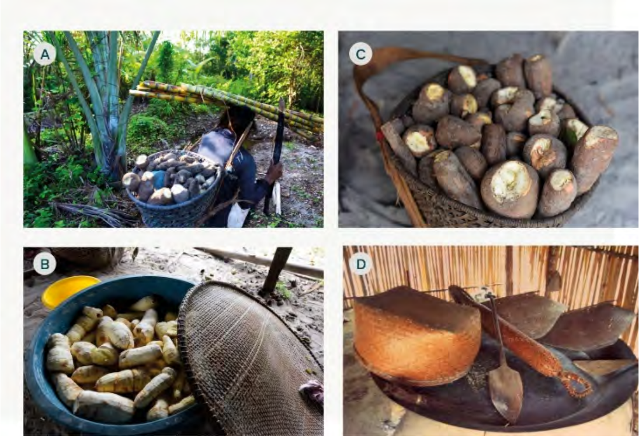

Figure 10.6 Bitter manioc processing among the Baniwa Indigenous people in the Upper Rio Negro, Brazil. Bitter manioc is harvested from a swidden garden on the upper Rio Negro (A) and brought back to the household for processing (B). Cyanide-containing bitter manioc is peeled (C), grated, pressed and sieved to remove water-soluble toxins using an extensive technology of baskets (D) made of *Ischnosiphon* spp (Marantaceae) and other plant fibers. Photos by Glenn Shepard, 2018.

Agroecology combines the principles of ecology with the traditional knowledge of Indigenous groups, local communities, and small farmers into a sustainable production system that protects agrobiodiversity and ecosystem services and values food security and sovereignty (Holt-Giménez and Altieri 2013). Agroforestry systems are considered a critical and viable economic option for conserving and restoring forest ecosystems worldwide (IPBES 2018). Given the tremendous erosion of global crop genetic diversity, attributed in part to the green revolution and agribusiness, the Amazon region is critically important for in-situ agrobiodiversity conservation (Steward 2013; Cunha and Lima 2016).

10.5.2. Fisheries and aquatic management

Freshwater fisheries play a critical role in sustaining Amazonian economies, cultures, and livelihoods. The Amazon Basin accounts for approximately 20% of the world's freshwater biodiversity (Lévêque et al. 2008), which is now critically threatened by commercial fisheries, land-use and livelihood changes, climate change, exotic species, hydroelectric dams and other large infrastructure projects, and mining operations (Doria et al. 2017; Goulding et al. 2019, see Part 2). With vanishing fish diversity and increasing river impoundment and degradation, associated ILK and specific fishing techniques are also being lost at a fast pace (Doria et al. 2017).

Traditional fishing strategies in the Amazon vary according to river type (white-water, black-water, clear-water), seasonal flooding regimes, and other livelihoods, including agriculture, hunting, animal husbandry, and extractivism (McGrath et al. 1993). The Amazon's floodplain ecosystems supported large pre-colonial Indigenous populations and remain important to regional economies owing to their fertile soils and abundance of aquatic resources (Roosevelt et al. 1996; McGrath et al. 1993; Goulding et al. 2019).

Fish species move beyond geopolitical frontiers, making it a difficult resource to manage. Seasonal fish migrations cross over numerous administrative and national boundaries, and between protected and non-protected areas, requiring social-ecological approaches and integrated coordination among Amazonian countries, which is seriously lacking (Doria et al. 2017; Goulding et al. 2019). Available research suggests IPLCs can plan an important role in understanding the diversity, ecology, and management of fish and other aquatic resources (Chernela 1994; Begossi et al. 1999; Ortega et al. 2001; Doria et al. 2017).

10.5.3. Hunting

Hunting is an important livelihood strategy among Amazonian IPLCs, but since productivity is generally lower for tropical forests than open habitats, overhunting has been considered a major threat to biodiversity in the Amazon (Bennett and Robinson 2000). Excessive hunting can have significant, wide-reaching impacts on the ecosystem by disrupting seed dispersion, predation, and herbivory (Wright 2003; Peres et al. 2016). Moreover, deforestation, habitat fragmentation, and agricultural expansion exacerbate impacts, for example when forest fragments are "emptied" of key species

(Redford and Feinsinger 2003; Francesconi et al. 2018; Ponta et al. 2019).

Some IPLCs' hunting practices and cosmologies emphasize checks, balances, and reciprocal exchanges between humans and prey species that would appear to restrain excessive hunting (Reichel-Dolmatoff 1976; Ross 1978; Shepard 2014; Vieira et al. 2017). However, the introduction of firearms to all but the most isolated Indigenous peoples and the commercial hunting of some species (Antunes et al. 2016) has drastically increased the impact of subsistence hunting, contributing to growing defaunation around established settlements (Jerozolimski and Peres 2003; Shepard et al. 2012; Boubli et al. 2020).

Yet, several Amazonian Indigenous groups maintain cosmologies, restrictions, food taboos, and other biocultural practices that may prevent overhunting. For instance, the Eñepa (Panare) of Venezuela avoid hunting near certain mountains considered to be the abodes of spirits who protect game animals (Zent and Zent 2018). The Ye'kuana rotate hunting zones and "rest" certain zones to allow game animals to recuperate (Hames 1980). Indigenous peoples of the upper Xingu observe some of the most extensive game animal taboos in the Amazon, contributing to the local abundance of large primates, tapir, and other harvest-sensitive mammals (Carneiro 1978; Shepard et al. 2012).

10.5.4. Brazil nut extractivism

The Brazil nut (*Bertholletia excelsa*) is the most important non-timber forest product of the Amazon (Duchelle et al. 2011), providing seasonal economic inputs to local, national, and international markets for tens of thousands of smallholders (Bojanic 2001; Peres et al. 2003; Kainer et al. 2007; Quaedvlieg et al. 2014). Brazil has historically been the main producer, but in 2018 Bolivia was the top exporter of Brazil nuts ($228M), followed by Peru ($65M), and Brazil ($60M) (OEC 2021). Brazil nut groves are especially abundant and intensely managed in the tri-national border area between Madre de Dios in Peru, the Brazilian state of Acre, and the department of Pando in Bolivia (Bakx 1988; Stoian 2000; Mittermeier et al. 2003). Brazil nut grove management has played an important role in resolving land conflicts, limiting deforestation, and providing sustainable economic activities in this region (Allegretti 2008; Cronkleton and Pacheco 2010). On the other hand, the current land use is a consequence of historical land use (for rubber) which promoted permanent occupation of *terra firme* forests, the ideal habitat for both Brazil nut and rubber (Chapter 11). Collaborative access arrangements, growing international demand, and organic certification have made Brazil nut a cornerstone of the region's economy and conservation efforts.

Archaeological data documents the consumption of Brazil nuts as early as 11,000 years ago (Roosevelt et al. 1996), and a preponderance of genetic, ecological, and ethnobotanical evidence suggests that the current basin-wide range of the Brazil nut has been significantly affected by human management practices (Shepard and Ramirez 2011; Scoles and Gribel 2011). Comparison of Indigenous language terms for Brazil nut throughout the Amazon has contributed to the reconstruction of possible routes of human-induced dispersal, providing another example of the links between language, culture, and biodiversity (Figure 10.8; Shepard and Ramirez 2011).

10.6. Governance and policymaking

The livelihood strategies and relationships of Amazonian IPLCs with biodiversity and the landscape involve a multiplicity of forms of governance. Here, we define governance as the set of rules, norms, and customary laws (or institutions) used by Indigenous peoples and local communities to a) access, use, manage, circulate, and market biodiversity; b) occupy the territory; c) make decisions about land and the territory; d) relate to nation states and other actors; and e) achieve self-determination (Sefa Dei and Restoule 2018). This multiplicity is based on a diversity of socio-cosmological systems

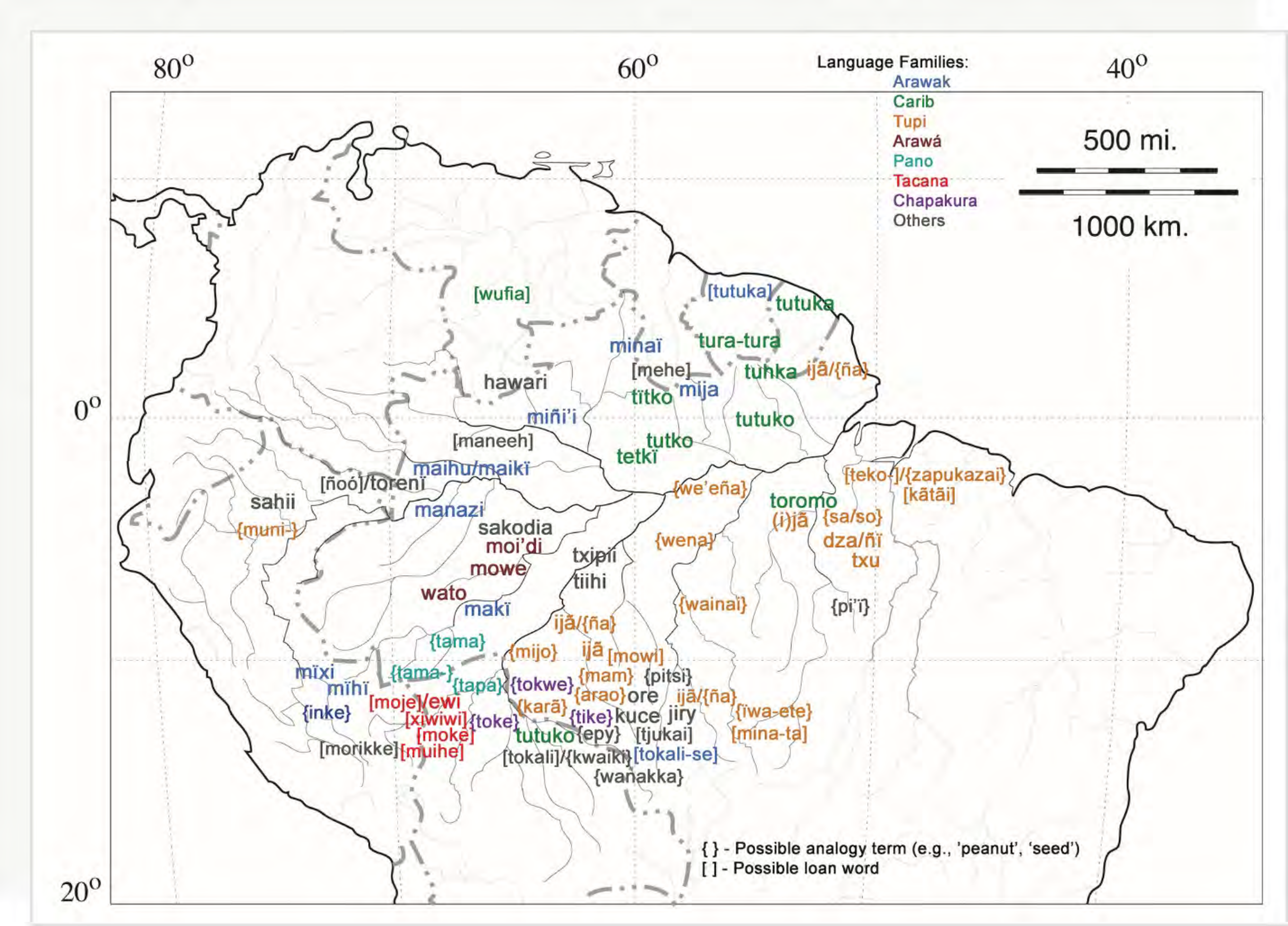

Figure 10.7 Indigenous terms for Brazil nut (*Bertholetia excelsa*) across several Indigenous peoples across the Amazon. Source: Shepard and Ramirez (2011).

and livelihood regimes, and it is expressed through various arrangements of communal institutions and collaborative relations, articulated or not with modes of state and private governance.

In fact, the main common feature of Amazonian IPLCs' socio-environmental governance systems is that they are organized in different regimes of communal governance of biodiversity, historically established in the different forms of territorial use, and are based on socio-political arrangements and diverse ecological knowledge regimes in their relations with animals, plants, fungi, minerals, and spirits (Diegues 1998; Lu, 2006; Futemma and Brondizio 2003; Stronza 2009; Almeida 2012; Castro 2020; Capelari et al. 2020). At the same time, such forms of governance are articulated with IPLCs' worldviews and cosmologies that, as we saw in previous sections, define living beings by their vital principles and the inseparability between nature and culture (Kohn 2013).

These Indigenous and local governance systems are often at odds with the laws and regulations of nation states, requiring new forms of socio-political organization (Erazo 2013; Athayde and Schmink 2014). Erazo (2013) noted the challenges faced by the Kichwa people from Ecuador to conform to the Ecuadorian Agrarian Reform and Colonization law, which created tensions between people's existing obligations to their kin group and their obligations toward a larger group of organizational members and leaders, a situation which continues to the present day.

Analysis of communal forms of governance emerged after the ecological debate on biodiversity conservation with the publication of the article The Tragedy of Commons (Hardin 1968). Harding stated that in communal governance arrangements, understood by the author as open access, individuals led inexorably to the depletion of natural resources. However, since the early 1980s, an increasing number of scholars have documented examples of biodiversity and spaces shared in common. These studies have shown that various IPLCs' communal strategies are based on a set of norms, values, institutional arrangements, and world-views that often have the potential to generate sustainable community management of biodiversity over the long term (Feeny et al. 1990; McKean and Ostrom 1995; Agrawal 2014; Ostrom 2015). The most significant contribution of "commons" studies has been to show that a multiplicity of regimes of communal governance can be defined as dynamic collective institutional arrangements that regulate the access, use, management, circulation, and control of biodiversity for food, wood, medicines, rituals, fertilizers, and fuel, as well as access to resources for spiritual and religious practices (Ostrom et al. 1994; Diegues and Moreira 2001; McKean and Ostrom 2001).

There are many examples of commons governance by IPLCs in the Amazon, linked mainly to forest agroextractivism, hunting practices, and fishing along lakes and rivers, but these governance systems are sparsely documented (Futemma and Brondizio 2003; Lu 2006). In the landscape of Amazonian "commons", biodiversity is appropriated by a well-defined community of users that have the power to define resource use rights mechanisms in communal regimes, establishing rules, incentives, and penalties, as well as including or excluding other users through local regulations.

In the pluri-ethnic riverine communities of the Puranga-Conquista (RDS) Sustainable Development Reserve in Rio Negro, Brazil, the household is the basic socio-political unit of the community. Heads of households are responsible for managing and negotiating access and control of spaces and natural resources that they are using directly. In general, each family has a set of cultivated spaces and forests that are for their use and possession. Fishing, hunting, and forest areas are managed at the community level. In this case, the community created governance mechanisms that allow access to the territory by all members of the community and exclude access to others. At the broadest level, with the creation of the RDS, a new governance model was instituted, with co-participation between the community and the State. In this case, governance was carried out through collegial and legal instruments of co-management, such as councils and management plans (Cardoso et al. 2008). Such a trans-scalar model that articulates household management with a network of relatives and allies reaching to the community level can be seen in several modes of (re)territorialization by Amazonian IPLCs (MacDonald 1995; Little 2003; Lu 2006).

Artisanal fishing communities of the Middle Amazon River provide a "laboratory" in which it is possible to explore examples of communal regimes. According to Pereira (2000), in this region some communities have autonomous local governance to regulate their fishing practices whereas others do not. Of those that do, some control only access to fishing grounds, while others control both access and the level of individual resource appropriation. In some communities, there is widespread adherence to management schemes, and in others, opposition threatens to destroy management institutions and deplete local fish stocks. In the case of a community floodplain fishery in the Peruvian Amazon, the resource institution was active at creating rules and means to keep outsiders out of the fishery. During an initial period of external threat, when fishing activity was high, governance was employed to create rules on allowed fishing techniques and seasons (Pinedo et al. 2000). However, for Lu (2016), interest and participation in the institution waned with the dissipation of the external threat and because of internal conflict. Such common arrangements in fishery activities are based on local configurations of kinship, local notions of territoriality, ecological knowledge, the formation of alliances, and mutual respect among actors. Such arrangements have been threatened since the 1970s, mainly in Brazil and Peru (McGrath et al. 1993; Pinedo et al. 2000; Pereira 2000), when the "war of the lakes'' began. This was a result of the modernization of the fishing fleet and State-granted permission to access IPLCs' territories, generating conflicts, modes of resistance, and requiring the subsequent creation of instruments of co-governance between communities and the State to mitigate conflicts.

Fishing agreements (*acordos de pesca*) and community governance (Isaac and Barthem 1995; Pinedo et al. 2000; Castro and MacGraph 2001; MacGraph et al 2008) systems to regulate *Arapaima gigas* by Indigenous peoples in the Juruá river (Figure 10.9) and riverine communities in the Mamirauá Reserve can be considered success stories of collective management (Castello et al 2008; Campos-Silva and Peres 2016; Campos-Silva et al 2017). These cases illustrate the problems and potential solutions of co-management schemes in artisanal fisheries as a means of amplifying stock abundance and lake productivity, by limiting exploitation by larger, often external commercial boats, while improving the quality of life for artisanal fishers and their communities.

Local communal arrangements can also be seen among IPLCs that practice forest and agroforestry. For Lu (2001, 2016), who studied the commons in Ecuador, the consistency of responses within communities suggests the existence of institutional arrangements that influence the way that agriculture is practiced. In communities that practice individual property arrangements, large tracts of land ranging from 20 to 200 hectares have been divided among households and the rights to the remaining land area are maintained by the household. In contrast, in communities with communal property arrangements, households only gain withdrawal rights to the lands they have cleared and cultivated, which are significantly smaller than those of individual property arrangement households.

These Amazonian systems of biodiversity governance have been under tremendous pressure, as 'commoners' are losing access to the territory and biodiversity, often through violent expropriation (MacDonald 1995; Lu 2016; Begotti and Peres 2020), shaping what many authors call the "tragedy of commoners" or "tragedy of enclosures" (Ortega Santos 2002; Molina and Martínez-Alier 2001). Such pressures are owing to the advance on the forest, with processes of land privatization, infrastructure construction, and agropastoral and mineral exploitation of Amazonian resources, with consequent impact on IPLCs' communal modes of governance. But, because of these pressures, in some cases, political mobilization and the institution of social movements by IPLCs has led to social resistance and reaffirmation of traditional communal appropriation regimes in Amazonian countries (MacDonald 1995; Allegretti and Schmink 2009; Silva and Postero 2020).

Some of these communal territorial governance regimes have been recognized and incorporated into the national constitutions of Amazonian countries in the form of territorial and cultural rights, or as models of *buen vivir*, *bem viver*, or living well, as in the case of Indigenous peoples in Ecuador and Bolivia (Acosta 2016; Gudynas and Acosta 2011) and Brazil (Schlemer at al 2017; Baniwa 2019). These rights have generally taken the form of three main tenure types: a) Indigenous reserves under which a group is given legal communal land title to large areas containing multiple communities; b) community tenure in which communities are given legal title through customary land tenure laws established for colonists; and c) protected areas, under which the state maintains public ownership of land in protected areas but grants legal use rights to Indigenous or community residents (Richards 1997).

The complexity and scale of environmental problems promote various types of collective and collaborative governance strategies between actors, given the impossibility of addressing them on their

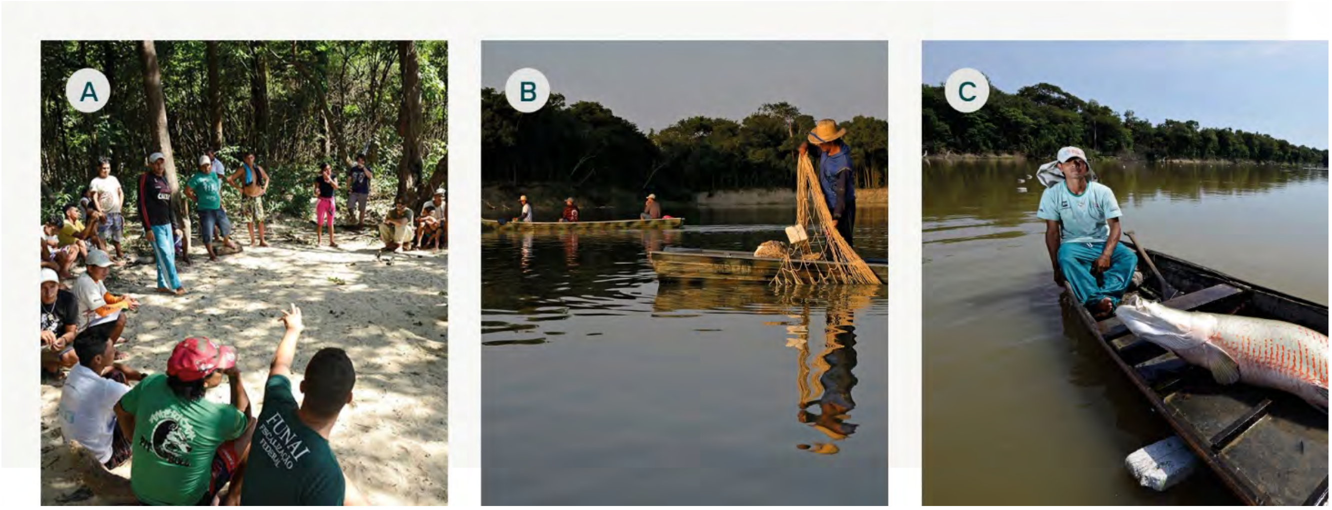

Figure 10.8 Co-management of *Arapaima gigas* (*Pirarucu*) by the Paumari Indigenous people in the State of Amazonas, Brazil. A. Meeting to coordinate lake and fishing management activities. B. Traditional fishing techniques used by Paumari Indigenous fishers. C. Abimael Chagas Cassiano Paumari showing a large *Pirarucu* captured in the Tapauá River. Photos by Adriano Gambarini, archive Operação Amazônia Nativa – OPAN.

own. Therefore, effective collaboration is an important item on the research and policymaking agenda, which can contribute to the design of more equitable and sustainable long-term collaborative initiatives between government, civil society, and IPLCs for achieving common goals, as well as implementing forest-based economies and nature-based solutions for the region.

10.7. Conclusions

Recognizing the multiple interconnections between socio-cultural and biological diversity in the Amazon is essential to sustainability and environmental justice for the Basin as a whole. Biocultural diversity in the region is manifested in IPLCs languages, worldviews, livelihoods, and deep historical entanglements with Amazonian plants, animals, and ecosystems. The valorization and maintenance of these lifeways in Indigenous territories, local communities, and urban centers is of critical importance for the conservation of Amazonian sociobiodiversity and the future of life on Earth for at least three main reasons. Firstly, the empirical and philosophical underpinnings of Indigenous and local knowledge systems provide key concepts and practices for developing a deeper, more historyically and socially situated understanding of the Amazon in its interconnected biological, ecological, and cultural dimensions. This includes first-hand knowledge and information about plant and animal species, sustainable management practices, and climate resilience (Heckenberger et al. 2008; Schwartzman et al. 2013). Secondly, Amazonian peoples maintain sophisticated knowledge about sustainably managing diverse agricultural, aqua-tic, and agroforestry systems, which in turn have dynamically shaped the region's ecosystems. Certain elements of Amazonian landscapes and biodiversity that were once considered "natural," such as Brazil nut groves, açai palm stands, and other economically-important "hyperdominant" plants bear the imprint of long-term manipulation, domestication, and management by Indigenous peoples (Heckenberger et al. 2008; Clement et al. 2010; Shepard and Ramirez 2011; Balée 2013; Clement 2019, Cross-Chapter 31.A). ILK systems have been, and should remain, instrumental in identifying and managing useful plant and animal species, contributing to global agricultural diversity, sustainably managing forests for subsistence and market-based economies, as well as innovative approaches to social-ecological restoration, climate change mitigation, and bioeconomy initiatives (Parts 2 and 3). Thirdly, IPLCs across the Amazon are holders of diverse world-views, values, institutions, and governance systems, all of which must contribute to shaping culturally plural, inclusive, and democratic societies. According to the UN Declaration on the Rights of Indigenous Peoples (UNDRIP 2007, supported by all Amazonian countries), IPLCs have the right to self-determination; they should be free to determine their political status and pursue their economic, social, and cultural development. IPLCs' languages, customary laws, institutions, and decision-making structures have resulted in the successful governance of their lands and territories for decades, if not centuries, and should continue to contribute to the implementation of Sustainable Development Goals (SDGs), the Convention of Biological Diversity's Post-2020 Global Biodiversity Framework, and other international policies of biodiversity conservation, environmental justice, and sustainable development.

Diversity, in all its forms, must be understood as a value to be cherished, nourished, promoted, and protected. Biocultural diversity in the Amazon and elsewhere provides the entire globe with knowledge, resources, alternatives, and innovations for addressing uncertainty as we navigate turbulent times and the social-ecological tipping points of the Earth's resilience. The Amazon is a living biocultural system that cannot survive without the valorization, empowerment, and participation of the diverse societies that have flourished among its rivers, forests, savannas, and estuaries.

10.8. Recommendations

- Support the recognition of land, territorial, and socio-cultural rights of Indigenous peoples, Afro-descendant communities, and other local communities, in connection to policies that value and support forest and water-based livelihoods, including economic incentives and credit for non-timber forest products.
- Support the documentation and preservation of Amazonian Indigenous languages and associated knowledge systems as living manifestations of endangered biocultural diversity.
- Develop policies for raising public awareness about Amazonian languages, including concrete actions for linguistic revitalization and conservation integrated with biodiversity conservation policies.
- Promote applied research on agrobiodiversity connected to food security and sovereignty among Amazonian IPLCs, respecting associated biocultural relationships and intellectual property rights.
- Recognize and support women's leadership and role in agrobiodiversity conservation and resource management in the Amazon.
- Support forest-based and ecosystem-based livelihoods in the Amazon through economic incentives, policies, and regulations.
- Support the protection of the territories of Indigenous peoples in voluntary isolation.

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Amazon Assessment Report 2021

Chapter 11

Economic drivers in the Amazon from the 19th century to the 1970s

Gado e visto em área de fazenda próximo a floresta (Foto: Bruno Kelly/Amazônia Real)

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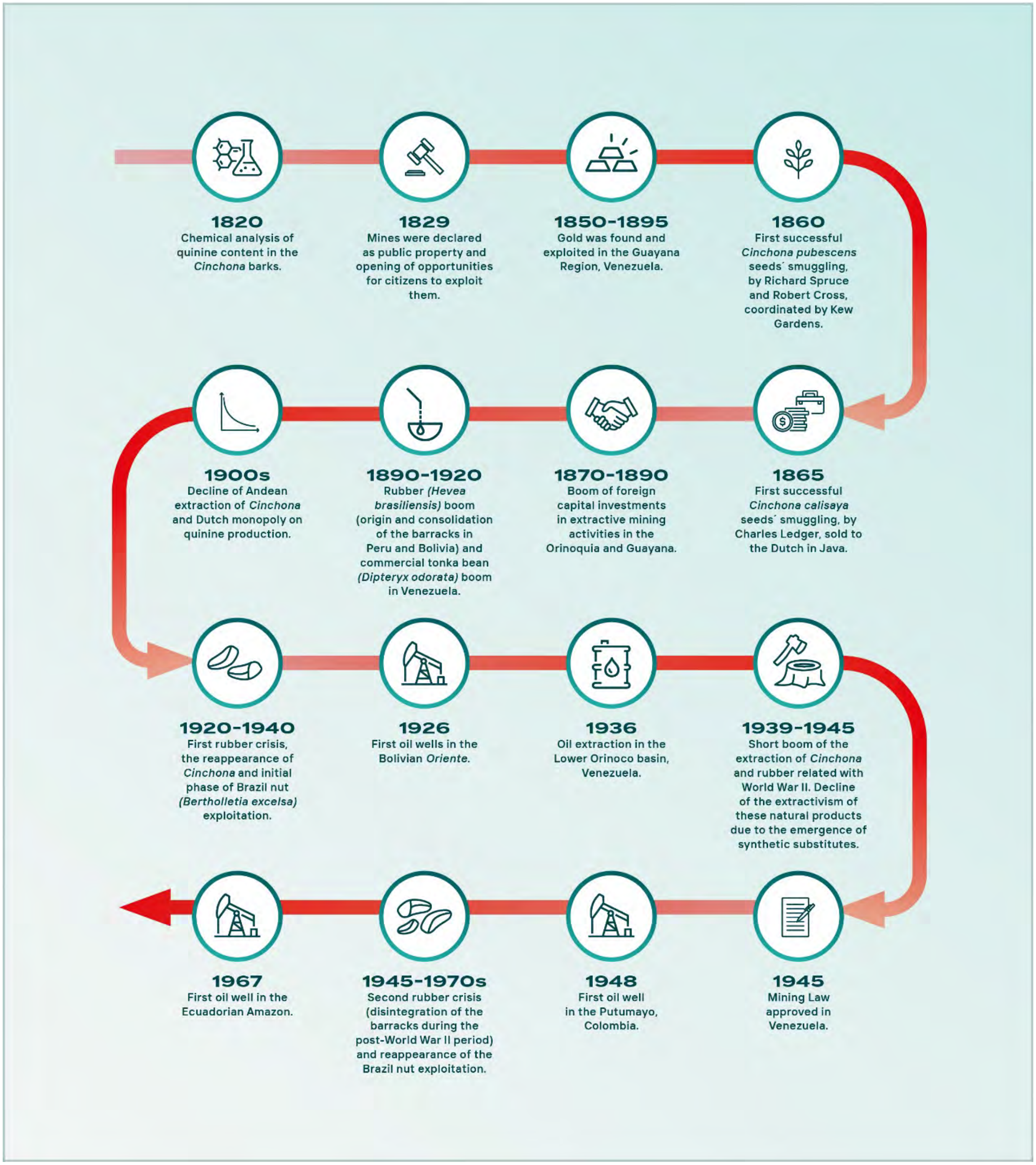
Graphical Abstract



1820
Chemical analysis of quinine content in the *Cinchona* barks.

1829
Mines were declared as public property and opening of opportunities for citizens to exploit them.

1850-1895
Gold was found and exploited in the Guayana Region, Venezuela.

1860
First successful *Cinchona pubescens* seeds´ smuggling, by Richard Spruce and Robert Cross, coordinated by Kew Gardens.

1865
First successful *Cinchona calisaya* seeds´ smuggling, by Charles Ledger, sold to the Dutch in Java.

1870-1890
Boom of foreign capital investments in extractive mining activities in the Orinoquia and Guayana.

1890-1920
Rubber *(Hevea brasiliensis)* boom (origin and consolidation of the barracks in Peru and Bolivia) and commercial tonka bean *(Dipteryx odorata)* boom in Venezuela.

1900s
Decline of Andean extraction of *Cinchona* and Dutch monopoly on quinine production.

1920-1940
First rubber crisis, the reappearance of *Cinchona* and initial phase of Brazil nut *(Bertholletia excelsa)* exploitation.

1926
First oil wells in the Bolivian *Oriente.*

1936
Oil extraction in the Lower Orinoco basin, Venezuela.

1939-1945
Short boom of the extraction of *Cinchona* and rubber related with World War II. Decline of the extractivism of these natural products due to the emergence of synthetic substitutes.

1945
Mining Law approved in Venezuela.

1948
First oil well in the Putumayo, Colombia.

1945-1970s
Second rubber crisis (disintegration of the barracks during the post-World War II period) and reappearance of the Brazil nut exploitation.

1967
First oil well in the Ecuadorian Amazon.

Figure 11.A Graphical Abstract

Economic Drivers in the Amazon after European Colonization from the Nineteenth Century to the Middle of the Twentieth Century (the 1970s)

Daniel M. Larrea-Alcázar[a], Nicolás Cuvi[b]*, Judson F. Valentim[c], Luisa Diaz[d], Silvia Vidal[e], Germán Palacio[f]*

Key Messages

- During the nineteenth and twentieth centuries, there were boom and bust cycles for various natural products such as *Cinchona* and rubber. Processes such as the extraction of gold continued, and the exploitation of oil was initiated, both continuing to this day. The extraction of some products created the conditions necessary for the exploitation of others, as in the shift from Chichona to rubber and then from rubber to the Brazil nut.
- Extractive industries were always supported by States, in association with national and foreign investors, and took advantage of Indigenous labor, often in exploitative conditions. Access to the Amazon and the extraction of these products initially took place using rivers, which also continues in the present, with the addition of roads and highways since the twentieth century.

Abstract

The objective of this chapter is to identify the main economic processes that occurred in the Brazilian, Andean, and Guyanese Amazon during the nineteenth and twentieth centuries until the 1970s. Specifically, the chapter describes the history of extractivism and the effects of geopolitical reconfiguration in the Amazon after the processes of emancipation or decolonization. It analyses the history of the extraction of natural resources, starting with quina barks (species of the genus *Chinchona,* Rubiaceae) and rubber (*Hevea brasiliensis*, Euphorbiacae), as well as the characteristics and practices developed by social actors related to the local and regional economy that arose from these exploitations. It also includes a synthesis of the history of exploitation of oil, minerals (mainly gold), wildlife trafficking, the emergence of mechanized agriculture, intensive livestock herding, and mega-infrastructure. Finally, it identifies the main lessons learned and key messages from the use of "historical commodities" in the Amazon and their implications for contemporary patterns of use of resources, such as the Brazil nut (*Bertholletia excelsa*, Lecythidaceae).

Keywords: History of extractivism, Cinchona, rubber, oil, natural gas, gold, NTPF.

11.1. Introduction

Over the last two centuries, the Amazon's oil, minerals, and biodiversity have been used intensively as a result of national and international economic interests. Public policies promoted by Amazonian countries have sought to ensure sovereignty and, gradually, private and state investment, creating a complex configuration of socioecological systems (Homma 2003; Hecht 2011; Bottazzi *et al.* 2014; Pinho *et al.* 2015), even creating "parallel states" (Cuvi 2011; Hecht 2011; Hecht and Cockburn 2011).

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In the nineteenth and twentieth centuries, examples of “parallel states” were those derived from the extraction of non-timber forest products such as *Chinchona* spp. or rubber (*Hevea brasiliensis*) in Brazil, Bolivia, Colombia, Ecuador, and Peru (Hvalkof 2000; Homma 2003; Hecht and Cockburn 2011). These processes affected current patterns of use and occupation (Hecht 2011; Schmink 2011), including violations of the rights of Indigenous peoples and other settlers who were used as low-cost labor in the region. The so-called eco-harvest of the Brazil nut (*Bertholletia excelsa*, Lecythidaceae), currently one of the economic engines of the southwestern Amazon (Peru, Brazil, and Bolivia), is a legacy of the rubber period, which in turn was a legacy of the *Cinchona* period (Stoian 2000, 2005; Duchelle *et al.* 2012).

Since the early 1960s, the predominant perception among the national governments about their Amazon territories was that there were empty, unused spaces, with formidable natural resource reserves (e.g., minerals, oil, hydroelectric energy, wood, agriculture, and plants for pharmaceutical, cosmetic, and agrochemical uses) and with their sovereignty at risk (Fearnside 1987; Hecht 2011; Clement *et al.* 2015). Several countries established policies and programs with the objective of occupying and accelerating the integration of the Amazon into national and regional economies (Fearnside 1987; Valentim and Vosti 2005). This was achieved through the construction of new roads, improvement of existing roads, and investments in large hydroelectric plants, mainly in Brazil. Governments also provided tax incentives and subsidized credit for private investment in oil and mineral extraction, extensive agriculture, and livestock projects (Valentim and Vosti 2005). Policies promoted large-scale initiatives linked to government and private settlements for the relocation of landless families from other parts of their countries (Valentim and Vosti 2005; Hecht and Cockburn 2011; Valentim 2015; Fearnside 2016). In Brazil, these initiatives were complemented by a pilot project for the implementation of an Industrial Free Zone in the city of Manaus, capital of the state of Amazonas (Aloise and Macke 2017).

These policies and processes accelerated socioeconomic and environmental changes from the early 1960s to the late 1970s. These changes were characterized by rapid population growth in rural and urban areas, accompanied by increased deforestation and urbanization (Valentim and Vosti 2005). As the myth of the Amazon as an empty, unused space was discredited, there was a sharp increase in territorial conflicts between new settlers and Indigenous peoples and local communities (Valentim and Vosti 2005; Hecht and Cockburn 2011). Towards the end of the 1970s, there were a large number of conflicts over land rights and natural resources, which went hand in hand with a growing global perception of the Amazon’s key and fundamental role in global sustainability (Hecht 2011; Schmink 2011). This led to the emergence of organized socioeconomic movements that, in association with the growth and effectiveness of national and international political actions, continue to struggle to reshape existing social policies and new ecological systems towards sustainable and inclusive development of the Amazon (Hecht 2011; Schmink 2011).

This chapter synthesizes the main historical processes as economic drivers that shaped the current landscape and diversity of socioecological systems in the Amazon. It carefully analyses what happened after European colonization, from the nineteenth century to the emergence of national sovereignty projects between the 1950s and 1970s. The main natural resources that were used in this period are described, including a synthesis of those resources that today are part of the economic engines of the region.

11.2. History of the Extractive Economy Based on Quina

“Quina” or “cascarilla” are the most frequent names for the plants of the genus *Cinchona*, and some of the genera *Remijia* and *Ladenbergia*. Their barks, in the form of powders, have medicinal properties including the ability to prevent and treat malaria (Achan *et al.* 2011) (Figure 11.1). *Cinchona* bark contains four main medicinal alkaloids: cinchonine, cinchonidine, quinidine, and quinine, the last being the most important. Each species has different concentrations of alkaloids, which can vary even within the same species depending on the locality, altitude, soil type, age of the tree, and harvest time. There is also a lot of hybridization between species (Garmendia 2005; Maldonado *et al.* 2017). The genus *Cinchona* is widely distributed in the tropical Andes, from the lowlands to above 3,000 m (Figure 11.2 and 11.4). Only the *C. pubescens* species reaches the mountains of Panama and Costa Rica. The sites with the greatest diversity and endemism are southern Ecuador and central Peru (Andersson 1998). The quinas have sometimes been called the "savior plants of mankind". Over time they became important icons for various nations, finding a place in the national emblem of Peru in 1825, and becoming the national plant of Ecuador in 1936 (Acosta 2019).

Like many other historical and contemporary products, the history of the quinas connects the Andes and the Amazon with the world at different times. This history is made up of religious, commercial, and scientific controversies. For example, debates have taken place for centuries as to whether Indigenous peoples knew about its medicinal properties (see for example, Ruiz 1792 or von Humboldt 1821); in this regard, there is increasing evidence that knowledge was transmitted from natives to Jesuits (Estrella 1994; Ortiz Crespo 1994; Crawford 2016). An erroneous history that has circulated widely, up until the present day, refers to the fact that the Countess of Chinchón was cured of malaria with powders of *Cinchona* bark and then she distributed it to the peoples of Lima. Today we know that this story is full of errors, beginning with the supposed participation of the Countess (Haggis 1941). However, it served the purpose of validating the medicine among the nobility and the people. The first European explorer to describe these plants was the French academic Charles Marie de La Condamine, who sent specimens to Linnaeus (de la Condamine [1738] 1986). The Swedish botanist gave that Latin name to the plants, convinced of the legend of the Countess of Chinchón. Shortly after, Joseph de Jussieu carried out a more detailed exploration, but his work was not widely known (Jussieu [1737] 1936). After them, more explorers hunted for quinas in South America (WHMM 1930).

Figure 11.1 Glass pharmacy jar containing powdered quinine. Source: Unknown maker, Wellcome Collection. The jar is believed to be from the pharmacy of the Milosrdnych Bratri Monastery and Hospital Brno, in the Czech Republic. The painted label written in Latin indicates that this glass pharmacy jar contained powdered quinine. In: https://wellcomecollection.org/works/ycqazud9

The connections of the quinas account for the appetite of several international markets, which first led to intensive extractivism and then to the successful smuggling of seeds to Asia, after several attempts by European monarchies and republics since the 18th century (Brockway 1979; Spruce 1996). European colonization of the interior of Africa was fundamental in increasing demand

(Headrick 1981). *Cinchona* was a decisive incentive for the opening of roads to and in the Amazon, later used for other products such as rubber.

The *C. officinalis* species from Loja, in southern Ecuador, also called "fine *Cinchona*", was the first to be extracted in the 17th century. Due to the growing demand, the *Cinchona* areas of that region were rapidly destroyed, generating lucrative businesses and early warnings about the destructive processes associated with the extraction of bark (Espejo and Estrella 1993). The 18th century witnessed boom and bust processes in Cuenca and Loja (Moya Torres 1994). In the eighteenth-century, demand was so high that the Spanish crown monopolized the product for 38 years (Puig-Samper 1991; Estrella 1994; Crawford 2016) and sent two great botanical expeditions to New Granada and Peru, one of whose main objectives was the discovery of anti-malarial plants. One aim of that royal expeditions was to determine if Loja's fine bark trees were present in other sites, or to find equally effective species (Caldas 1966; Nieto Olarte and Flórez Malagón 2001) Those expeditions helped to increase the knowledge of *Cinchona* to a large extent, but also contributed to the intensification of conflicts around the taxonomy, distribution, and quality of the different species (Fernández 2019). Even the Prussian Alexander von Humboldt intervened in the matter, further confusing the issue and, as in other matters, without giving explicit recognition to the sources of his knowledge (Cuvi 2011).

There was much controversy over the quality of the quinas, an issue associated with frequent adulterations (Crawford 2007). That situation changed in 1820 when the alkaloid quinine was first isolated by Pierre-Joseph Pelletier and Joseph B. Caventou, which led to improved analysis. After that, it was possible to measure the quality of different species, and to open new sites for extraction in Ecuador, Peru, and Colombia, where it helped configure an Andean-Amazonian space, generating profound transformations of the landscape (Figure 11.3). In those countries, there were three periods of boom, of which the third, between 1877 and 1882, mainly in Santander and on the Amazon slope and foothills, allowed for improvement of the fragile links between the Amazon and the country and laid the foundations for subsequent rubber exploitation (Zárate Botía 2001; Palacio Castañeda 2006). Chemical analysis also led to the knowledge that one of the species with the highest quinine content was *C. calisaya*, distributed at altitudes between 200 and 3,300 m, especially in Bolivia towards the Amazon slope, intensively exploited from the beginning of the nineteenth century (Steere 1943; An-

Figure 11.2 The *Cinchona* regions of South America, nineteenth century. Source: Clements R. Markham, Peruvian bark: a popular account of the introduction of chinchona cultivation into British India, 1860-1880. Welcome Collection. In https://wellcomecollection.org/works/hjgh4e7c

Figure 11.3 Gathering and drying of *Cinchona* bark in a Peruvian forest. Source: Wood engraving, by C. Leplante, c. 1867, after Faguet. Wellcome Collection. https://wellcomecollection.org/works/werf33s3

dersson 1998; Zárate Botía 2001; Maldonado *et al.*2017). As in Colombia, the use of this species laid the foundations for the subsequent exploitation of rubber, by involving the native population in its exploitation, defining an economy strongly based on free access and low-cost labor.

In several enclaves, such as the Cuenca and Loja regions in Ecuador, and in Colombia, Peru, and Bolivia, there was a direct relationship between political power and "*cascarilleros*" (bark gathereres) (Moya Torres 1994; Zárate Botía 2001). The quinas were fundamental in opening up mountain passages towards the Amazon, in addition to strengthening existing ones and motivating the migration of locals and foreigners into the Amazon. Extractive areas proliferated throughout the Amazon. Among other things, transportation routes changed, no longer moving through the Andes and ports such as Callao, Guayaquil, or Cartagena; but also through the Amazon, via Iquitos or Manaus, boosting local economies. It triggered large-scale spatial, social, and economic changes, fostering a whole series of production chains, from the packaging of bark to the provision of food, meat, bananas, sugar cane, cocoa, coffee, cotton, cassava, yam, oats, fruit trees, tobacco, and livestock (Zárate Botía 2001). Bolivia even decreed a monopoly on *Cinchona* and created a Bank of *Cinchona* in 1840 (Pardo Valle 1947).

Among the main users of *Cinchona* bark were the expansionist European empires, who needed it for their armies in Africa and Asia. They had been trying to smuggle plants since at least the 17th century, finally succeeding in 1860, when *C. pubescens* seeds were sent from Ecuador to Sri Lanka and India (Spruce 1996), and in 1865 when seeds of *C. calisaya* from Bolivia arrived in the Dutch colonies on the island of Java. The British used the alkaloid-poor *C. pubescens* species to make totaquina, while the Dutch received seeds from the powerful *C. calisaya*, which they genetically improved, increasing its quality and creating a new species, *C. ledgeriana*, named in honor of smuggler Charles Ledger, who illegally obtained the seeds from Manuel Incra Mamani, an Indigenous man from Bolivia (Gramiccia 1988).

Towards the end of the nineteenth century, South American production reached its peak, and gradually began to stagnate, because Dutch production in Java monopolized the market and British purchases declined. By the first half of the twentieth century, Java accounted for 90-95% of the global production and market. Only small shipments departed from South America, representing a marginal percentage of production, sometimes bought out by members of the Kina Bureau to take them off the market (Pardo Valle 1947). When it stopped being profitable, the quineros' investments found different targets. In Bolivia and Colombia they became rubber barons (Stoian 2005). In Colombia, they also directed their financial capital into the coffee and navigation sectors (Zárate Botía 2001).

During World War II there was a brief, although very intensive, renewed boom in the extraction of Andean quinas (Hodge 1948; Cuvi 2011). This led to the reopening or rearrangement of routes from the mountains to the Amazon, also associated with other renewed extractivist actions such as those involving rubber (Bangham 1945; Cuvi 2011). An important case comes from Tingo María, in Peru, where, among other things, a colonization front associated with a scientific station was made. During this period, Colombia was the largest supplier of bark, followed by Ecuador, Bolivia, and Peru. The scale of the *Cinchona* Program was unprecedented. In the 18th century, when the Spanish crown exercised a 38-year monopoly over the production of *Cinchona*, 350,000 pounds of bark were shipped to the Royal Apothecary (de Andrés Turrión 1989). In contrast, through the *Cinchona* Program, between 1941 and 1947, the United States imported approximately 40 million pounds of dried bark. This figure does not include bark processed in Latin American factories (Cuvi 2011).

Quinine and other natural anti-malarial alkaloids obtained from *Cinchona* barks remain an important antimalarial drug almost 400 years after their efficacy was scientifically documented, although in a much lower amount. Since World War II, synthetic compounds such as chloroquine or primaquine, among others, have been widely used (Greenwood 1995). The same can be said for synthetic quinine, used since 1944 (Woodward and Doering 1945). There were a few subsequent booms, for example during the Vietnam War, when synthetic-resistant strains of malaria appeared (Greenwood 1995). However, over time demand for the natural product declined considerably, limiting its use to beverages such as tonic water, cosmetics, or medicines to combat resistant strains.

Cinchona alkaloids were among the first Andean-Amazonian products to be integrated into European therapeutics. These processes contributed to myths about the potential riches of South America (see Chapter 9), whose products were gradually and constantly incorporated into international markets. The boom-and-bust cycles illustrate how demand from these markets impacted not only the products themselves, but also the forests that contain them, and local economic, social, communicational, political, and geopolitical dynamics. Today we can identify similar cases around *guayusa* and *ayahuasca*, among other products. The case also illustrates the long duration of biopiracy, a process that we still witness, for example, with the bioprospecting of useful plants.

The decrease in demand for South American *quinares* since the nineteenth century, first owing to the development of plantations in southeast Asia, then to the decrease in demand for natural bark, has changed the status of the *Cinchona* plants, which moved from being on the verge of extinction to not currently threatened. Only one of them, *C. mutisii*, is considered Endangered according to the IUCN Red List, and three others are Vulnerable. Today, pressure comes from the continuous destruction of habitat.

11.3. History of the Extractive Economy of Rubber

In the nineteenth century, European capitalism had already established a framework to search for and transfer wild plants that were potentially useful as raw materials for industry and in pharmacy. Although the natives of the Amazon Basin demonstrated the use of rubber products to arriving Europeans since the sixteenth century, it was not until the discovery of vulcanization in 1839 that industrial application of rubber multiplied and a boom in demand took place. Among the many latex producing species worldwide, those belonging to the genus *Hevea*, especially *H. brasiliensis* (Euphorbiaceae) provide the highest yield of the highest quality latex. The fast-growing world rubber demand led to a boom in rubber production in the Amazon.

Although rubber production ("the trees that produce gold", Zeitum Lopez 1991) involves a large number of the countries, its history is linked to the lowlands of Brazil, Peru, and Bolivia) (Figure 11.4). In 1880, the Amazon Basin was the only place in the world producing wild rubber. Brazil supplied 60% and Peru 30% of global rubber consumption (Haring 1986). In Peru, the rubber economy coincides in part with the so-called period of the "Aristocratic Republic (1895 - 1919)", after the Pacific War (1879 - 1883), when the country lost territory and access to its exportable renewable resources, guano and saltpeter, to Chile (Contreras and Cueto 2013). The defeat was a strong blow to Peru's economy and position as the primary exporter of these materials, causing economic collapse (Pennano 1988). Without guano and saltpeter, Peru turned to other economic activities, such as rubber exploitation in the Peruvian Amazon. This period saw the global consolidation of capitalism, which implied the search for regions in the world that could supply natural resources to major economic powers, as well as the establishment of unequal commercial relationships between countries (Chirif 2011). Peru formed part of this unequal economic model as a supply country. In the case of Bolivia, the use of rubber began at the start of 1860. It was characterized by the fact that many families dedicated to quina, already in decline, moved to rubber. They promoted production based on the establishment of barracks that allowed them access and direct control over the forest, as well as to consolidate Indigenous labor, giving rise to unequal employer-client relations (Stoian 2005). The rubber boom in Bolivia occurred between 1898 and 1919 and was characterized by high prices rather than volume, an incentive for the involvement of private capital, mainly foreign, and a state that benefitted from the collection of taxes without exercising any control over the rights of the forest (Stoian 2005). In Brazil, this cycle started in 1850 and crashed towards 1920 (Weinstein 1983; Dean 1987).

In 1896, the Peruvian merchant Julio Cesar Arana began exploring rubber plantations in the Putumayo River valley, now a territory of Colombia. By 1905, he had acquired over three million hectares within Colombian territory, using Indigenous labor to extract rubber. Over the course of twelve years during which native rubber was exploited, the Indigenous population of this region went from 30 thousand to less than eight thousand, while revenues of US $75 million were generated from the export of 4,000 tons of rubber. In Brazil, rubber export houses were mainly concentrated in the cities of Manaus (state of Amazonas) and Belem (state of Pará), which were the main ports of the Amazon River system. At its peak, rubber was one of the leading products in the Brazilian economy, accounting for up to 40% of its exports, second only to coffee (Weinstein 1983; Dean 1987; Becker 1995). In 1876, Henry Alexander Wickham, working for the Royal Botanical Garden of London, collected 70,000 rubber tree seeds in the Tapajós River Valley and took them to England. The resulting seedlings were later planted in British colonies in Malaysia, generating extensive, high-yielding plantations. Over a period of 50 years, the British became the largest rubber producers in the world, with disastrous effects on the Amazon's economy.

In Peru, the rubber economy was based in the city of Iquitos, which collected rubber from the surrounding areas. Transport between Iquitos and Lima, over the Andes, was difficult. For this reason, Iquitos was naturally more connected to markets by the Amazon River. This connection increased after 1853 when an agreement was reached with Brazil for the navigation, circulation, and trade of Peruvian ships on the Amazon River (Pennano 1988), and commercial relationships were also established with England and the United States. By this time, Charles Goodyear had discovered the vulcanization of rubber (1839), and international demand rose, making Brazil the first and most important producer of this product. The city of Iquitos, Peru, achieved its rubber economic boom after Manaus (Chirif 2011). Export records show that the export of rubber grew exponentially from 1862 to 1870, and again from 1884 to 1910, although the following year, 1911, there was a sudden export decline due to falling international prices (García 1982; de la Rosa 2004).

In Peru, rubber was exploited in the Putumayo Basin (now Colombian territory), and in the Madre de Dios region, where an intensive search for new rubber-producing areas took place. In Putumayo and Madre de Dios, this activity disrupted the lives of local Amazonian populations, who were captured, subjected to slavery, and massacred ("Putumayo massacres") in order to extract rubber and meet growing international demands (García 1982; Casement 2014). Towards 1870, as demand grew, the harvesting of rubber spread to new areas and led to the rise of Iquitos and Manaus as large rubber centers. At the same time, in Madre de Dios new routes were sought for the extraction and trade of rubber (de la Rosa 2004). Ancestral knowledge about the management of rubber forests was used (Pennano 1988), and those who had that knowledge were enslaved.

The Amazon was integrated into the global economic order, supplying rubber to distant economic centers and establishing trade relations between countries (Chirif 2011). In the case of Bolivia, the rubber economy was concentrated in the north of the Amazon (along the Yata, Mamore, Itenez, Orthon, Tahumanu, and Madre de Dios Rivers). Its decisive and key participant was the so-called "Casa Suarez" (Nicolas Suarez and his brothers) that based its success on control of the vertical supply chain (of meat and other foodstuffs) for the barracks and laborers, along with a system of debt-peonage (in Spanish "*habilito*", in Portuguese "*aviamento*"), which became widespread throughout the region and persists today in the case of the Brazil nut (*B. excelsa*). On the other hand, Casa Suarez bet on the control of the transport route (eg. Cachuela Esperanza, Beni) and then on the control and administration of the territory, specifically, the barracks (Weinstein 1983; Stoian 2000, 2005).

In both Peru and Bolivia, before intensive rubber exploitation was established, local populations went deep into the Amazon to extract latex using native techniques. It was then transformed and transported to small shipping ports for sale (Pennano 1988; Stoian 2000, 2005). In the case of Peru, specifically Putumayo, native manual labor was used for this extraction, while in Madre de Dios both Andean migrants and local Indigenous populations participated (García 1982; Pennano 1988). Around 1890, with the increase in this activity, the *Regatón* figure appeared, which later became the *aviador*, thus monopolizing the local rubber trade (Pennano 1988). As the *aviador* knew the needs of the rubber collectors, he granted them credit on account of future collection, but added interest to the loan. The *aviador* easily found the backing of a banker to trade the rubber while, over time, the local producers could not repay the loans and were left in debt-peonage, at the expense of the *aviador*. In both countries, the first rubber colonies were made up of a boss, rubber tappers, and peons (García 1982; Stoian 2005). The boss was the owner, who paid a fixed salary to the rubber tappers, while the peons, mostly Indigenous, received a piece-rate payment, condemning them to permanent debt-peonage with no power to leave. The rubber economy was based on a local chain economic system, in which the rubber tapper depended on commercial companies for credit, employed workers to take care of the land, and, in some cases, semi-enslaved Indigenous people for the direct extractive work (Stoian 2005 and others).

Rubber seeds were also taken from the Americas, creating large plantations in other colonies, which were equipped with roads, railways, cheaper labor, and better possibilities to reach international markets. The opposite happened in South America, except for isolated trials by Harvey Firestone and Henry Ford in Brazil or Roberto Crawford (Pichis River) in Peru (San Román 1994). On the Amazon and Napo Rivers, rubber estates were created from relatively small legal grants of land, which became joint ventures that commercialized rubber and agricultural products (Weinstein 1983; Becker 1995). On the border of Brazil, Peru, and Colombia, powerful rubber exploitation lineages were established and came into constant conflict with one another, while a border dispute between Peru and Bolivia in Madre de Dios was permanently fueled by the expansion of rubber production. Returning to the commercial *boom* developed in Iquitos (Peru), Cachuela Esperanza (Bolivia), and Acre (Brazil), its success was based on a regional commercial monopoly, led by companies or powerful families with investment capacity, access to credit, and channels and incentives to export (Weinstein 1983).

During the twentieth century, World War II interrupted the supply of cultivated rubber from Southeast Asia to the Allied Forces and increased demand for rubber from collectors who extracted latex from native rubber trees scattered throughout the Amazon. In response to this demand, the Brazilian government organized the “Battle for Rubber” to increase rubber production in the Amazon. More than 30,000 “rubber soldiers” were recruited, mainly from the northeast region of Brazil, and sent to work in the Amazon’s rubber plantations. With the end of World War II, most of the financial support from international governments for these projects was stopped, and the region’s economy faced a decline that lasted almost two decades, affecting not only Brazil but also Peru and Bolivia (Weinstein 1983; Dean 1987; Pennano 1988; Stoian 2000, 2005). The extractivist economy based on the exploitation of rubber completed the integration of the Amazon into the world economy; however, it depended heavily on the decline in *Cinchona*, participation of foreign capital, and a system of barracks that was gradually consolidated and remained “intact” for decades. It was also later deeply affected by the reorganization of access to forest resources and the redistribution of land by agrarian reform processes, especially in Peru, Bolivia, and Brazil.

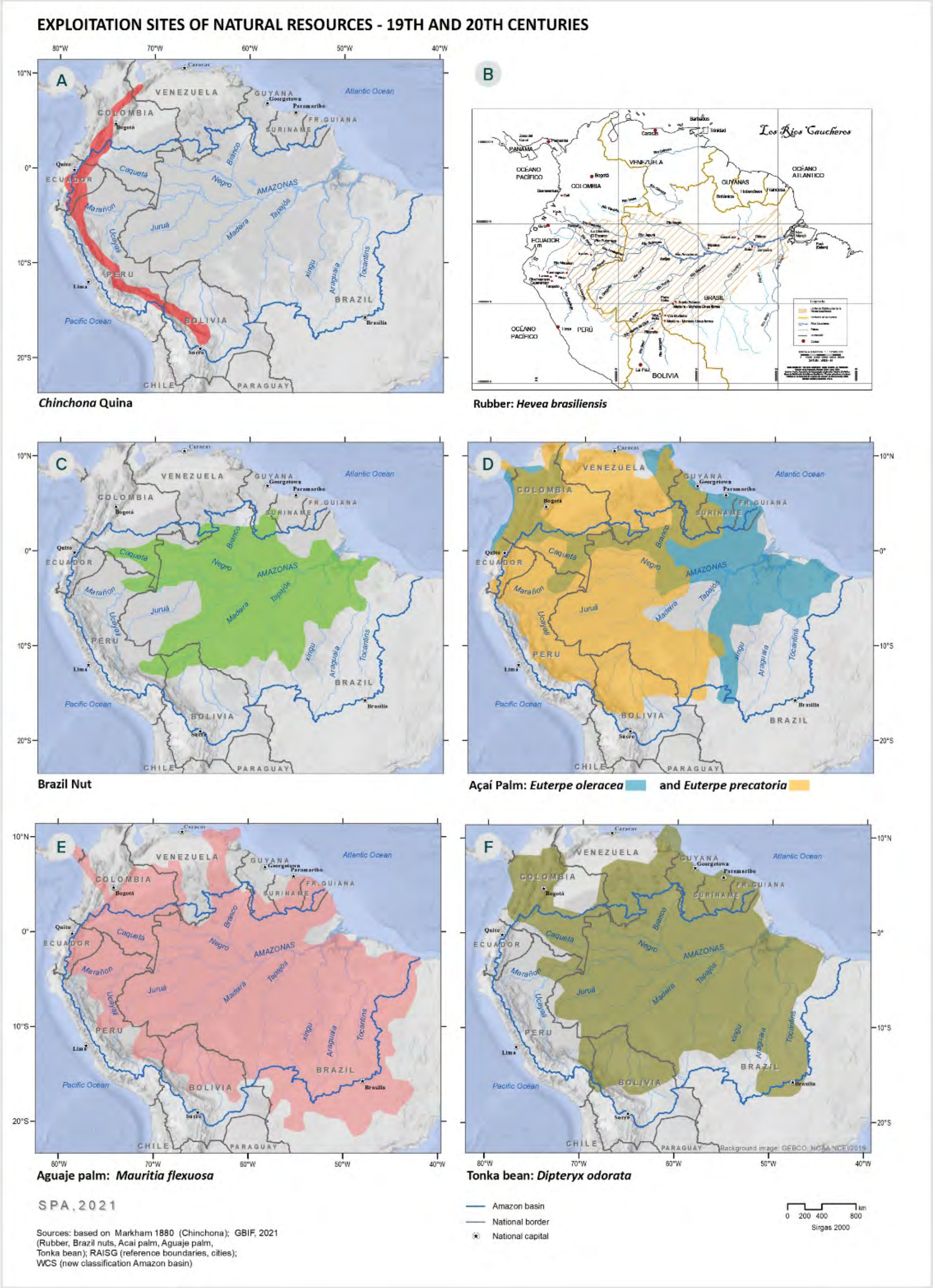
11.4. Other “Commodities” from the Amazon: Wildlife and Non-Timber Products

In pre-Hispanic times, the flora and fauna of the Amazon were objects of consumption and trade across the American continent, under the control of different Amerindian peoples and while conserving biodiversity (Chernela 1985; Lopez-Zent 1998). However, since the nineteenth century, global industrialization and the imposition of extractive economic models shifted the balance to have a negative impact on ecosystems and local populations. An enormous amount of wildlife from the Amazon has been exported to the United States, Europe, and Asia to meet demand for leather, skins, and feathers, among other products. This has caused the extinction of several species and threatens others. The eight Amazonian countries have made lists of threatened species of flora and fauna, which include more than 12,000 native species (Sinovas *et al.* 2017), such as timber and non-timber plants, including cedars, mahogany, palm trees, lianas, vines, and orchids; as well as small and large animals such as reptiles, mammals, fish, and frogs. These species are sought after for industrial (pharmaceutical, food, cosmetic, textile, fashion, furniture), medicinal, and ornamental purposes, as well as for the pet market.

National governments have enacted laws and legal measures have been taken to reduce this pressure on native biodiversity, such as the creation of forest reserves or protected areas, regulation of the hunting of certain species, and the breeding of plants and animals in nurseries and captivity for commercialization. However, the lucrative, uncontrolled, and illegal extraction of wildlife continues to exist (Mayor *et al.* 2007; Rodríguez and García 2008). During the 16th and 17th centuries, some animal species were traded, such as the manatee (*Trichechus inunguis*) for its meat, skin and oil, and the macaw (*Ara macao*) for its feathers and exotic flavor. Between the eighteenth and nineteenth centuries, the Amazon and Orinoco turtles were almost exterminated by the enormous collection of their eggs to make oils, just as the Orinoco caiman hunt began. From the middle of the nineteenth century to the beginning of the twentieth century, animals such as otters, hawksbills, eagles, and boas were caught for the export of their skins, antlers, and shells. Live birds were also caught for their plumage and as pets; birds, shrimp, snails, shell, and nacre lime were dissected; alligator, puma, and jaguar hides were stored; insects, oysters, ducks, pearls, and water and land turtles (morrocoy) were caught and their shells collected (Rodríguez and García 2008; Sinovas *et al.* 2017). During the 1920s in Bolivia, when rubber prices declined, trade in forest animal hides and skins rose and the "Casa Suárez" in Cachuela Esperanza became an important shipping point (Letellier 1964). In the 1970s, demand for wild fauna skins from the fashion catwalks increased. The same happened with butterflies, tarantulas, colorful frogs, lizards, snakes, ornamental birds, and fish such as paiche or pirarucú, among others, to be used as pets, for biomedical and ethological research, and for advertising aimed at tourists (Sinovas *et al.* 2017).

There was also a high demand for export of timber species, such as red cedar (*Cedrela odorata*) and mahogany (*Swietenia macrophylla*), primarily to the USA and Mexico. In Venezuela, due to the overexploitation of these species, the national government mandated the creation of forest reserves during the 1950s-1960s, but legal logging removed valuable timber species above the legal size and left the remnants damaged. Also, due to pressure from private companies, protections were weakened in many forest reserves. Domestic demand for these species increased sharply from 1946 to the 1960s. To meet demand, lower-quality species such as *Anacardium excelsum* ("mijao") and *Tabebuia rosea* ("apamate") were felled. In 1970, a system was started which temporarily granted time lots for the exploitation of timber in forest reserves, but these were used unscrupulously and illegally by logging companies, without any control or nurseries to promote the regeneration of timber trees (Kammesheidt *et al.* 2003). One example is the Imataca Forest Reserve, which extends through the states of Delta Amacuro and Bolívar, where the ancestral territories of several Indigenous peoples are located, and which was declared a World Heritage Site by the United Nations Educational, Scientific and Cultural Organization (UNESCO). Today, the Mining Arc has destroyed an important part of Imataca Reserve, where legal and illegal exploitation of various minerals and intense deforestation occur.

Furthermore, many non-timber plants of great importance for the biodiversity of tropical forests have great commercial appeal, including palm trees such as moriche palm (COL), aguaje palm (PER), palma real (BOL) (*Mauritia flexuosa*) (Figure. 11.4), mamure (*Heteropsis spruceana*), and chiquichique (*Leopoldinia piasava*) (Clement *et al.* 2015; Levis *et al.* 2017). Additionally, tonka bean trees (*Dipteryx odorata* and. *D. punctata*, Fabaceae), have been removed from forests in large numbers since the nineteenth century, thanks to their aromatic fruit used mainly in the perfume industry (Torrealba 2011). There are different species of tonka bean trees found in Brazil, Peru, Bolivia, Ecuador, Colombia, Trinidad, Venezuela, and the Guyanas (Torrealba 2011, Figure 11.4). In Venezuela, wild tonka bean trees ("sarrapia") are located in the Amazon, Bolívar, and Delta Amacuro States, but the highest concentration of trees ("sarrapiales") is found in Bolívar State, specifically in the Sucre and Cedeño municipalities, in the territory that expands from the northern Amazonas state, on the Suapure and Parguaza Rivers to the Bajo Caura. During the rubber era (1875-1920), in this region of Venezuela, a commercial tonka bean boom occ-



Chinchona Quina

Rubber: *Hevea brasiliensis*

Brazil Nut

Açaí Palm: *Euterpe oleracea* 🟦 and *Euterpe precatoria* 🟨

Aguaje palm: *Mauritia flexuosa*

Tonka bean: *Dipteryx odorata*

SPA, 2021

Sources: based on Markham 1880 (Chinchona); GBIF, 2021 (Rubber, Brazil nuts, Acai palm, Aguaje palm, Tonka bean); RAISG (reference boundaries, cities); WCS (new classification Amazon basin)

Figure 11.4 Areas of historical distribution of use of A) *Cinchona* (species of the genus *Chinchona*, Rubiaceae), B) rubber (*Hevea brasiliensis*, Euphorbiaceae)¹, C) Brazil nut (*Bertholletia excelsa*, Lecythidaceae), D) açai palm (*Euterpe precatoria*, Arecaceae), E) moriche/aguaje/palma real (*Mauritia flexuosa*, Arecaceae) and F) tonka bean (*Dipteryx odorata*, Fabaceae).

urred (Scaramelli and de Scaramelli 2005). Its commercialization process played an important role in the economic and cultural dynamics of various Indigenous peoples (Mapoyo, Panare, Piaroa and Jiwi) and some Middle Orinoco peasants. Its use was followed by migratory waves of workers from different parts of Venezuela in the period 1890-1965, with significant demand during the consolidation of the extractive economy in Guyana and the institutionalization of debt-peonage (Torrealba 2011). Its production is still in force on a smaller scale. Its seeds have always been highly valued by Europe and the United States and have been widely used in the manufacture of perfumes, the tobacco industry, the pharmaceutical industry, and in food production. The upper Amazon was the center of domestication and origin of cocoa (Zarrillo *et al.* 2018), which was also grown and used in the southeast of present-day Ecuador. In both colonial and early post-colonial times, the coast had the largest number of cocoa plantations, which reached their peak production in the late nineteenth and early twentieth centuries and then collapsed due to pests (McCook 2002). To this day, the Amazonian territories represent only a marginal proportion of national cocoa production.

Following intense extraction of *Cinchona* during the nineteenth century, and rubber at the beginning of the last century, is the harvest of the Brazil nut (Figures 11.4). The rubber period left behind an Amazonian territory characterized by the appearance and dilution of the "barracks" and the formation of new rural settlements (Stoian 2000, 2005). The Pará region in Brazil is largely covered by the Tocantins basin where Brazil nut harvesting began in the middle of the nineteenth century (Clement *et al.* 2015; Levis *et al.* 2017). There are records that mention the export of Brazil nut to Europe as early as the seventeenth century, and although the harvest was relatively intense in Brazil after the collapse of the rubber industry, lower operating and labor costs ended up favoring production in the Madre de Dios region (Peru), and Pando and Riberalta (Bolivia), the main Brazil nut exporting regions today (Clay 1994, 1997). In both regions, the emergence and consolidation of an extractivist economy based on Brazil nuts benefited from the socioeconomic context (agro-extractivism based on the collection of raw materials from the forest) and knowledge and use of the forest generated from the legacy of rubber production (Stoian 2000, 2005).

It is important to highlight the Pará region, to which the name of the Brazil nut alludes, since other species of contemporary economic importance historically come from this region. This includes the açai palm (*Euterpe oleracea,* Arecaceae*,* Figure 11.4), a name that comes from the Indigenous word Iaçá, which written backwards is açai, whose fruits were important elements in the diet of the Indigenous peoples of the central Amazon. The palm hearts of several species of açai palm were exploited intensively during the 1940s in Brazil's south and southeast regions (*E. edulis* and *E. oleraceae*), even affecting other species during the 1960s and 1970s (*E. precatoria*). In the case of Bolivia, this continued until the 1990s (Stoian 2004, Figure 11.4). Its use was also a consequence of the collapse of the rubber industry (Stoian 2004, 2005). Market contraction, differences in cutting cycles and intensities, increasing distances between supply areas and processing plants, and the detection of botulism caused production to slowly diminish, giving way to species in managed systems, such as *Bactris gasipaes*. The intense use of palm hearts, and associated felling of palm trees, probably affected the populations of these species, especially *E. precatoria* (Johnson 1996; Stoian 2004). However, evaluations on this topic are scarce. On the other hand, in recent decades, supply, production, distribution, and export chains have been consolidated for the pulp or derivatives of açai fruits (*E. oleracea* and *E. precatoria*), especially in Brazil. Such processes are still being strengthened in other countries, such as Colombia and Bolivia.

Extractivism is part of the history, occupation, and re-occupation of the Amazon, as evidenced by an economy based on *Cinchona* and rubber in the recent past, and later on the tonka bean, açaí palm, and Brazil nut. During the nineteenth and twentieth centuries, such activities resulted from national security policies that promoted colonization of and migration to the Amazon, promoted by republics in the process of stabilization, especially Brazil, Ecuador, Venezuela, and Colombia. These occupation processes were decisive in initiating and consolidating the geography and geopolitics of large-scale exploitation, as is the case of rubber. Added to this were agrarian reform processes that took place from the middle of the last century, which defined new structures and configurations of land ownership. One example is the concept of *latifundios* (large estates) in the Bolivia lowlands that favored mechanized agriculture and intensive cattle raising, leaving extractive activities to peasant and Indigenous communities. On the other hand, dozens of promising NTFP species have been identified, many of them multi-purpose palm species part of the pre-Columbian history of the Amazon (Homma 1992; Clement *et al.* 2015; Levis *et al.* 2017). These products face the considerable challenge of becoming a viable alternative to deforestation and, in the case of Amazonian fruit species, domestication and commercialization through agroforestry systems.

11.5. Historical Gold Mining

Rumors about the immense natural riches of the Amazon began with European conquest (Simón 1882; Rivero 1883; Whitehead 1988). Various explorations confirmed the existence of metallic and non-metallic mineral deposits, including iron, gold, nickel, silver, coltan, thorium, clay, sand, limestone, bauxite, diamond, quartz, jade, titanium, dolomite, phosphate, granite, plaster, zinc, and copper (Tinoco 2000; Martiz 2019). The most influential and impactful mining has been, without a doubt, gold. Many current populations owe their existence to the fact that they were enclaves of exploitation of this resource. Legal and illegal gold mining coexist in the Amazon and relevant legislation has undergone significant modifications over the years. Europeans reported that Amerindians mined gold and traded it regionally and interregionally, in various communities of the Orinoco and Amazon (Whitehead 1990, 1991). In the 16th century, the colonial system established that mines were the property of the crown, and in 1783 the Mining Ordinances of New Spain expanded this to include precious stones, non-metallic minerals, and coal (Cartay 1988; Fernández 2001).

In the case of Venezuela, in 1829 Simón Bolívar decreed that mines were the property of the Republic and gave citizens the opportunity to exploit them under certain conditions set by the Federal Executive. In 1854, José Gregorio Monagas, then Governor of the Guayana region, enacted the first Mining Code of Venezuela, while his brother, José Tadeo Monagas, was president of the Republic (Martiz 2019). The most significant exploitation of minerals area occurred from 1850 to 1890. The first discoveries of gold, in the area of El Callao, led to applications for the first licenses, the registration of mines, and the installation of factories for the production of gold bullion (Baptista 1997; Paülo and Ángel 2006). This period was also characterized by a boom in foreign capital investments for mining (gold, iron, and oil), forest resources (balata, rubber), and transportation (railways and trams). In the case of Guyana, leading companies and factories for the processing of gold were created, such as Compañía Minera El Callao (1870), Compañía Austin (Orinoco Exploring and Mining), South America Mining. Co, Compañía Minera de Nacupay, Chile, Alianza de Cicapra, El Porvenir, Nueva Hansa, Potosí, Buen Retiro, San Salvador, and La Concordia (Torres 2001).

During the period 1866-1895, the deposits with the highest-grade ores in Venezuela were extracted (Torres 2001), and crushing mills with pylons were installed in the mines belonging to Nacupay, El Callao, Panamá, Mocupia, and Potosí. Gold Field of Venezuela LTD (1898-1946), an English company, bought part of the companies operating in the area and worked with the old mills of the Potosí company. Most of its gold was exported because Venezuela did not have enough processing plants to produce industrial parts. In 1945, the Mining Law was approved in Venezuela, in which mineral deposits were declared to be of public utility. However, institutional criteria in its application promoted corruption and other acts outside the law. In 1977, Decree 2039 was approved, eliminating the right to acquire a legal grant of land through a simple mining request (area delimited by UTM coordinates) to the authorities, along with free exploration and exploitation (Chacín 1998; Martiz 2019), increasing the accountability of the process.

In 1970, the Compañía General de Minería de Venezuela C.A. (CVG MINERVEN) was put in charge of investments and the modernization of mines, whose primary gold deposits in Bolívar state are located in Tumeremo, El Callao, El Dorado and El Manteco, in the Cuyuní River Basin and the regions drained by the Yuruarí, Botanamo, Caroni, Venamo, and Caura Rivers (Egaña 1979; Noguerol *et al.* 2000; Martiz 2019). Since the 1970s, these mining developments have had a significant impact on rivers, jungles, and savannas, as well as on Indigenous populations of the region, such as the Pemón, Yekuana, Sanemá, Lokono, and Warao. Also impacted were Afro-descendant towns located in the Caura basin, which originate from ancient "*cumbes*" (escaped slave hideout towns), due to the mass migration of miners from other areas of the country and abroad. Additionally, in the period 1970-1980, other gold deposits were found in Venezuela in the Ventuarí, Alto Orinoco, Atabapo, Guainía, Casiquiare, and Negro Rivers, in Amazonas state, and in Colombia in the mountains of Nakén (Guainía), Panapaná (Cuiarí), the hills of Taraira, and Vaupés (González Bermúdez 1996).

As happened in several areas of the Amazon, many young Indigenous people from different ethnic groups moved to work in both legal and illegal gold mines, abandoning jobs as teachers and nurses. This was only moderately profitable for them, or not profitable at all, due to the high cost of living and excessive work (González Bermúdez 1996). Some Indigenous families began to work mining alluvial gold, isolated and separate from the mines controlled by Creoles, but the proliferation of violence, arrival of merchants, prostitution, and alcohol generated conflict and confrontation. The significant immigration of non-Indigenous miners and their operations destroyed the environment, communities, and Indigenous territories and their economies, leading to murders, drug trafficking, and theft, as well as forms of modern slavery.

The destructive effects of legal and illegal or informal activity, of small- and large-scale mining, especially the chemical agents used in the processing of gold (mercury, cyanide) is well-known. In Venezuela, the instruments used in traditional, non-Indigenous mining were the shovel, pick, machete, and wooden tray. Extractivist companies and national governments have taken little interest in studying the system and methodology of exploitation of gold by Indigenous peoples, who knew how to conserve natural systems. In ancient times, they exploited gold, considered to be rays of sunlight (Whitehead 1990, 1991). They knew about goldsmithing and gold alloys (with silver and copper), making idols; geometric, anthropomorphic, and zoomorphic figures; personal adornments; and thin sheets of gold which functioned like currency in local and regional trade. For many Indigenous Carib and Arawak peoples today, the extraction of alluvial gold has no ritual restrictions. The exploitation of gold in open-pit mines or excavation requires rituals to obtain authorization from supernatural beings and ancestors, as tokens of respect and love for Mother Earth. These limitations on certain forms of mining are political actions to respect and protect the Amazon, which have been ignored by those who are only interested in the extraction of raw materials, dehumanizing local populations and destroying the Amazon.

Legal mining, with legislation that has undergone modifications over the years, has coexisted with illegal gold mining in the Amazon. Both have had substantial impacts on the geographies and situations of Indigenous, Afro-descendant, and peasant populations, among others (Whitehead 1990; Tinoco 2000; Arvelo-Jiménez 2014). Europeans reported seeing gold garments and jewelry that adorned members of the local elite and other Indigenous individuals. The original peoples of the Amazon practiced artisanal forms of mining, without causing destructive changes in the environment.

11.6. Historical Oil and gas Exploitation

Oil influenced the Amazon's economies during the twentieth century. It was essential for the consolidation of previous processes, such as those associated with the extraction of quina, rubber, and other products. In Latin America, few commodities have led to the same strong feelings of economic nationalism that arose in response to oil. The political debate has been dominated by critics and promoters of foreign multinationals' investment and participation, with oil policies fluctuating from open-door arrangements to nationalization and even expropriation of foreign-owned assets (Bucheli 2010).

Oil exploration in the Amazon dates back to the nineteenth century. However, in the Bolivian Lowlands (*Oriente)*, it only started in the 1920s (Klein 1964). In the Venezuelan *Orinoquía* exploitation has taken place since 1936, in the Colombian Amazon since the 1940s, in the Ecuadorian *Oriente* since the 1960s, and in Peru since the 1980s. Brazil has been a major consumer but a minor producer. These processes were marked by the intervention of international companies, sometimes with the participation of domestic ones, always in association with national elites. The degree of openness or national control has varied.

In the Bolivian *Oriente*, various explorations and attempts were made, first with national companies, then international ones (Klein 1964). After several unsuccessful attempts, in 1926 Standard Oil operated eleven production fields in the *Oriente* and others in various parts of the country. However, it had permanent conflicts with the State, related to noncompliance, clandestine installations, and other issues. In the 1930s, the outcome of the Chaco War, as in the subsequent Ecuador-Peru conflict, was related to conflicting interests between Standard Oil and Shell. In 1936, Bolivia created the company Yacimientos Petroliferos Fiscales Bolivianos (YPFB), which increased conflict by confiscating everything from Standard Oil, who requested intervention from the US government without much success (Klein 1964; Klein and Peres-Cajíias 2014). Natural gas occurs in the same fields as oil but only became economically important when foreign markets opened up. "Indeed, while the first records of natural gas production date back to 1952, it was not until 1972, with the start of exports to Argentina, that production reached significant levels" (Klein and Peres-Cajíias 2014). Since the 1970s, oil and gas have become fundamental engines for the Bolivian economy.

In Venezuela, oil was used by Indigenous peoples as medicine, for lighting houses, and for caulking canoes (Fundación Polar 2010). In 1800, Humboldt recorded the location of several fields in the region known as the Orinoco Belt Oil Fields (von Humboldt 1826; Fundación Polar 2010). The modern oil period began in 1875, with the founding of the national company Compañía Nacional Minera Petrólia del Táchira (González Rincones 1956). However, oil extraction in the Lower Orinoco Basin began in 1936, with Standard Oil and the drilling of the La Canoa-1 Well, in the southern areas of Guárico, Anzoátegui, Monagas, and Delta Amacuro (Fundación Polar 2010). In 1943, a Hydrocarbon Law was enacted, specifying the duration of licenses, taxes, and controls on foreign companies, which forced them to refine part of their production inside the country (Malavé Mata 1962). During the expansion of the Venezuelan oil industry since World War II, i.e., la Plaza 1980 (Quintero 1972), new types of licenses for export were created, as were "national reserves", the royalties from which resulted in an increase in the percentage of GDP from 15% in 1914, to 50% in the 1960s. Nationalization of oil production followed in 1976. Petróleos de Venezuela S.A. (PDVSA) was created, and that country became a founding member of the Organization of the Petroleum Exporting Countries (OPEC), generating high national profits.

As in other Amazonian countries, the oil boom had negative impacts on Indigenous peoples, such as the Kariñas. Although they possess colonial titles for land and received royalties from oil companies, they have had to migrate to other areas in the south of their territory owing to environmental deterioration, which has impoverished the economy and impaired health (Jiménez and Perozo 1994; Whitehead 1994; Arvelo-Jiménez 2014). In the 1960s, the closure of the Caño Mánamo, the main tributary of the Orinoco Delta, by the oil industry, caused flooding and an ecological disaster in wetlands, forests, and savannas, which destroyed the environmental, cultural, social, and economic balance of the Warao Indigenous people and caused impacts which persist until the present day (Heinen 1992).

In Colombia, the first exploitation of oil occurred on the coast, then in the Orinoquia, and finally in the Amazon. Putumayo's oil history dates back to 1937, with the Saxon Petroleum company. Texaco was in charge of the revitalization of this activity and in 1948 drilled the first well, José María 1, in the jurisdiction of Mocoa (today Puerto Guzmán). In 1955 the percentage of royalties that oil companies had to pay was reduced as a stimulus to explore the southern Amazon region, which led to Texaco obtaining a license for the exploration of 16,000 km² for 30 years in 1959, the most extensive given in Colombia until then. Texaco moved its work from the area near the Caquetá River to the border with Ecuador, where the Orito 1 well was drilled in 1963, becoming the epicenter of oil activity (completed in 1971) (Avellaneda Cusaría 2005).

Oil activity in Putumayo signaled the possibility of consolidating the country as an oil producer and articulating those territories to the nation. Oil activity made it possible to stimulate a new form of colonization, and transform the landscape in a more significant way than is generally attributed to peasant colonization, because the opening of roads led to a “sowing of people”. New municipalities, such as Orito, San Miguel, Valle del Guamuez, and Puerto Caicedo were created for the purpose of managing some royalties. There were investments in road infrastructure to connect extraction sites. Problems with land titling and ownership continue to cause conflict between residents and companies (Avellaneda Cusaría 2005).

Initial oil exploration in Ecuador took place in 1921. Geologists from the Leonard Exploration Co., a company that obtained a license for 50 years covering 25,000 km² (Wasson and Sinclair 1927), were ultimately unsuccessful, owing to a lack of funding (Gordillo 2003; Rivadeneira 2004). After that, Shell carried out explorations from 1938 (Tschopp 1953); after they obtained a ten-million-hectare license in 1937, they opened roads from the central Andes, built an airport, and caused significant impact on local Indigenous peoples. They did not find sufficiently lucrative deposits in terms of crude oil quality, and the exploitation had logistical difficulties due to its remote nature. After the 1941 war between Ecuador and Peru, which various people associated with the interests of competing oil companies, the former lost a large part of its territory, including the licensed area, so Shell retired in 1948 (Rivadeneira 2004).

After Shell left Ecuador, President Galo Plaza stated that “the *Oriente* is a myth”, adding that Ecuador was not designed to be an oil country but an agricultural one (Rivadeneira 2004). However, in 1968, the Texaco-Gulf Consortium, which in 1964 had obtained a license for 1.400 million hectares for 58 years (Ramón *et al.* 2019), began drilling high-quality fields in the northeastern zone, starting with the Lago Agrio 1 well in 1967. These explorations were successful, and the country began exporting crude oil in 1972. In part, this was made possible by the explorations carried out on the Colombian side of the Putumayo in 1963. The corporation built roads and an oil pipeline that crossed the Andes to the coast. It operated for almost 20 years with very little oversight, causing enormous pollution. The company acted as a parallel state in the territory. Other companies also explored diverse areas in the 1960s and 1970s. The *Oriente* ceased to be a myth and the oil rush and its related economic opportunities attracted thousands of migrants, some as part of the agrarian reform and colonization of 1973. These processes were widely criticized by some sectors of the population, including Jaime Galarza Zavala (1974), imprisoned by the ruling Military Junta for protesting. He alluded to the Seven Dinosaurs (Standard Oil of New Jersey, Shell, Mobil, Gulf, Texaco, BP, and Standard

Oil of California) that behaved as they pleased in the countries.

11.7. The Start of Intensive Cattle Ranching in the Amazon

Livestock, along with road construction and government-induced settlement programs, have been the main drivers of deforestation since the 1960s (Fearnside 1987; Valentim and Vosti 2005). Cattle were introduced to São Paulo, Brazil, from Cabo Verde (Africa) in 1534 (Homma 2003). In the mid-17th century, Portuguese settlers introduced cattle to the Brazilian Amazon. Initially, cattle were raised on grasslands established after the deforestation of areas around the city of Belem (Pará). For the next three centuries, until the 1960s, the island of Marajó, in Pará, was the main cattle ranching center in the Brazilian Amazon. Livestock farming was also carried out along the middle and lower sections of the Amazon River, mainly in extensive grazing systems on native pastures in higher portions of temporarily flooded areas (Dias-Filho and Lopes 2020). During this period, most of the major urban cities in the Amazon had to rely on imported meat, sometimes from other parts of the country or from abroad to meet demand. Because of the lack of roads, in many circumstances, meat was transported by air, leading to scarcity and high-cost products that were only accessible to the wealthiest segments of the population (Dias-Filho 2014; Dias-Filho and Lopes 2020).

Across Latin America, livestock expansion since the mid-19th century has largely been a story of the transformation of forests into cultivated pastures (Van Ausdal 2009). This environmental transformation became more relevant in the early 1960s, when national governments implemented policies to integrate the Amazon with the rest of their territories. In Brazil, these policies included the construction and improvement of roads, subsidies for agriculture, and impressive resettlement programs for landless rural families (Valentim and Vosti 2005; Hecht 2011; Dias-Filho 2014; Dias-Filho and Lopes 2020). Extensive ranching systems also became an important strategy for land grabbers and speculators to convert forests into cultivated pastures and claim unregulated public lands (Fearnside 1987), a process that continues to be an important driver of deforestation in the Amazon today (Stabile *et al.* 2020). By 1975, the cattle herd in the Brazilian Amazon had already reached seven million heads on 20 million hectares of pasture. The resulting livestock load of 0.35 animals per hectare was an indicator of a very extensive production system with low productivity (Valentim and de Andrade 2005).

This land development strategy was based almost entirely on the limited use of technology, in particular forage germplasm and pasture management options developed for and imported from regions with different environmental conditions (Dias-Filho 2014). Conversion of diversified forest ecosystems into extensive areas of homogeneous grasslands with exotic African grasses in tropical conditions with high temperatures and humidity resulted in cultivated grassland ecosystems with low resilience, which favored the proliferation of pests and diseases (Valentim and Moreira 2001). In addition, farmers adopted poor management practices, such as repeated burning in an attempt to control the regeneration of native herbaceous and wood species, as well as the invasion of exotic plant species (Serrão *et al.* 1979). Fire was also misused to try to control high numbers of pests, such as spittlebug (*Deois* sp. and *Zulia* sp.), causing rapid and severe degradation of pastures. Repeated burning favored nitrogen volatilization, nutrient leaching, and erosion of exposed soil, degrading grasslands three to five years after their establishment (Valentim 1989).

Even under these conditions, Margulis (2003) reported that beef cattle farming in the Brazilian Amazon, even with prices 15% to 20% lower than in São Paulo, had a 113% higher profitability. This was the result of substantially lower land and labor costs. Despite being profitable, livestock farming in the Amazon during the 1960s faced several problems, such as rapid and extensive degradation of pastures, lack of technical and management expertise among farmers, and insufficient and inadequate technical assistance (Valentim 1989; Valentim and de Andrade 2005).

Repairing degraded pastures was difficult and extremely expensive due to shortages of tractors, plows, and harrows, and the high cost of limescale and fertilizers. As a result, farmers accelerated deforestation to expand the area of pastures (Serrão *et al.* 1979). This was facilitated by a legal framework requiring Brazilian farmers to deforest and burn their pastures as proof that it was "productive land" to receive an ownership title from the government (Fearnside 1987; Valentim and de Andrade 2005). Additional economic incentives for deforestation (Fearnside 1987) included lower taxes for owners of deforested lands. National and international concerns about rising rates of deforestation in the late 1970s led to increasing pressure on governments to change policies that incentivized deforestation for ranching and agriculture in the Amazon (Valentim and Vosti 2005; Hecht 2011).

11.8. Origins of Large Roads and Hydroelectric Plants

The end of World War II resulted in a gradual reduction in policies aimed at ensuring an adequate and constant supply of strategic natural resources from the Amazon (McCann 1995). With some exceptions, since then, economic development policies have been dominated by the provision of financial aid and the implementation of deliberate trade-protectionist policies to support national and multinational industrial groups in import substitution and state-led industrialization frameworks (Bran-do 2012). Key to this shift were improvements in transport infrastructure and the reliable supply of low-cost energy.

Approximately 100 hydroelectric dams were built in the 1950s, 103 in the 1960s, and 151 in the 1970s and 1980s (Von Sperling 2012). However, the construction of dams on Amazonian rivers has provoked clashes between developers, government officials, Indigenous populations, and environmentalists (Von Sperling 2012). The Amazon Basin, approximately 60% of which is in Brazil, is the focus of a massive program of hydroelectric dam construction. If successful, these plans could eventually turn almost all of the Amazon's tributaries into a chain of reservoirs for hydroelectric production (Fearnside 2015). Rich in rivers, Brazil has always considered hydroelectric energy as a way of fulfilling its ambition of being a great world power (Moran 2016). Brazil has used hydroelectric power since the late nineteenth century, but the 1960s and 1970s set the stage for increased investment in the construction of large plants. Some of the largest Brazilian dams in operation are located in the Amazon and were planned or initiated during this period. This is the case of Belo Monte (11,181 MW), located on the Xingu River, and Tucuruí (8,370 MW), located on the Tocantins River, both important tributaries of the Amazon River (Fearnside 1999, 2006).

Road construction has also been a key method for national governments to ensure sovereignty and integrate Amazonian territories into national economies. Brazil began implementing an impressive policy of highway construction in the early 1950s, which accelerated after the 1964 military coup. Several of these highways, such as the Trans-Amazonica (BR-230), BR-163, and BR-319, are still in the process of improvement and paving, raising many concerns about their environmental and socioeconomic trade-offs (Valentim and Vosti 2005; Laurance *et al.* 2009; Moran 2016). This is particularly relevant as the density of roads in one county is associated with increased human migration and deforestation in that county and similar side effects in neighboring counties (Pfaff *et al.* 2007).

The construction of new roads in the Amazon also has important implications for previously isolated rural communities or Indigenous extractive communities affected by their construction (Riley-Powell *et al.* 2018). By the late 1970s, evaluations and concerns about past, present, and future socioeconomic and environmental impacts of policies that promoted the construction of roads and hydroelectric dams in the Amazon Basin were already on the rise, both in the Amazon and internationally. At the time, there was a growing debate among researchers and policy makers about the challenges and possible strategies for mitigating negative impacts to promote sustainable and inclusive development. Various economic processes were intensified throughout the Amazon starting in the 1970s; for example, oil extraction, deforestation, and hydroelectricity. This was accompanied, sometimes motivated by, the strengthening of land access routes and the consolidation or creation of cities. These processes continue to this day. The opening of land routes is accompanied by issues such as deforestation for timber and the opening of the agricultural frontier.

11.9. Conclusions

Most of the economic cycles of the Amazon between the nineteenth and twentieth centuries were motivated by the demand for raw materials from external markets, located in industrialized nations of the Global North. They were part of geopolitical and geographical processes in the emergence and consolidation of the republics. They had different degrees of participation by States, supported the emergence of powerful elites, and promoted the perception of Indigenous peoples and local communities as low-cost or even free labor (“dehumanization” of the Amazon). These extractive processes continue in part to this day, when products such as beef, oil, or soy, are produced especially for export from Amazonian countries.

The Amazon has witnessed cycles of rise (*boom*) and fall (*bust*) in the exploitation of raw materials, which have shaped diverse social, economic, and spatial structures, sometimes to the detriment of previous territorial arrangements. Products such as *Cinchona* and rubber led to the opening of waterways, roads, cities, settlements, and collection and distribution centers, as well as population movements. Economic booms associated with commodities attracted migrants who gradually took over territories, almost always to the detriment of ancestral populations.

There are two great continuities within the extractivist economy from the nineteenth century to 1970; 1) a neocolonial or postcolonial system derived from the extraction of raw materials, with enslaved or recruited cheap labor, for export, and 2) the management of lowland forests and ancient tropical savannas maintained by Indigenous, Afro and some peasant peoples. Without identifying, revaluing, and adopting the important contributions of Indigenous knowledge and practices to the management of the Amazon, the region will continue to be an heir of the colonial system, which today entails the irreversible destruction of forests and other ecosystems.

The Amazon has been seen as a reservoir of raw materials of strategic global value, particularly in times of crisis. In the 1950s, national governments started to promote occupation and integration of the Amazon, percieved as an empty region with its sovereignty at risk, through policies focusing on road construction; exploitation of minerals such as gold, oil and iron; hydroelectricity projects; resettlement of poor landless populations; and the promotion of deforestation and subsidized agriculture and cattle ranching projects.

11.10. Recommendations

- Looking to the future, we must learn from Indigenous groups and their thousands of years of successful, sustainable management and shaping of natural resources. How to develop economic models that avoid asymmetric exploitation practices, such as debt-peonage, is a key challenge.
- Various Andean-Amazonian products have generated enclave economies over the centuries, with boom-and-bust processes. Economic activities must be carried out within sustainability frameworks, guaranteeing the long-term well-being of Amazonian communities.

11.11. References

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Amazon Assessment Report 2021

Chapter 12

Languages of the Amazon: Dimensions of diversity

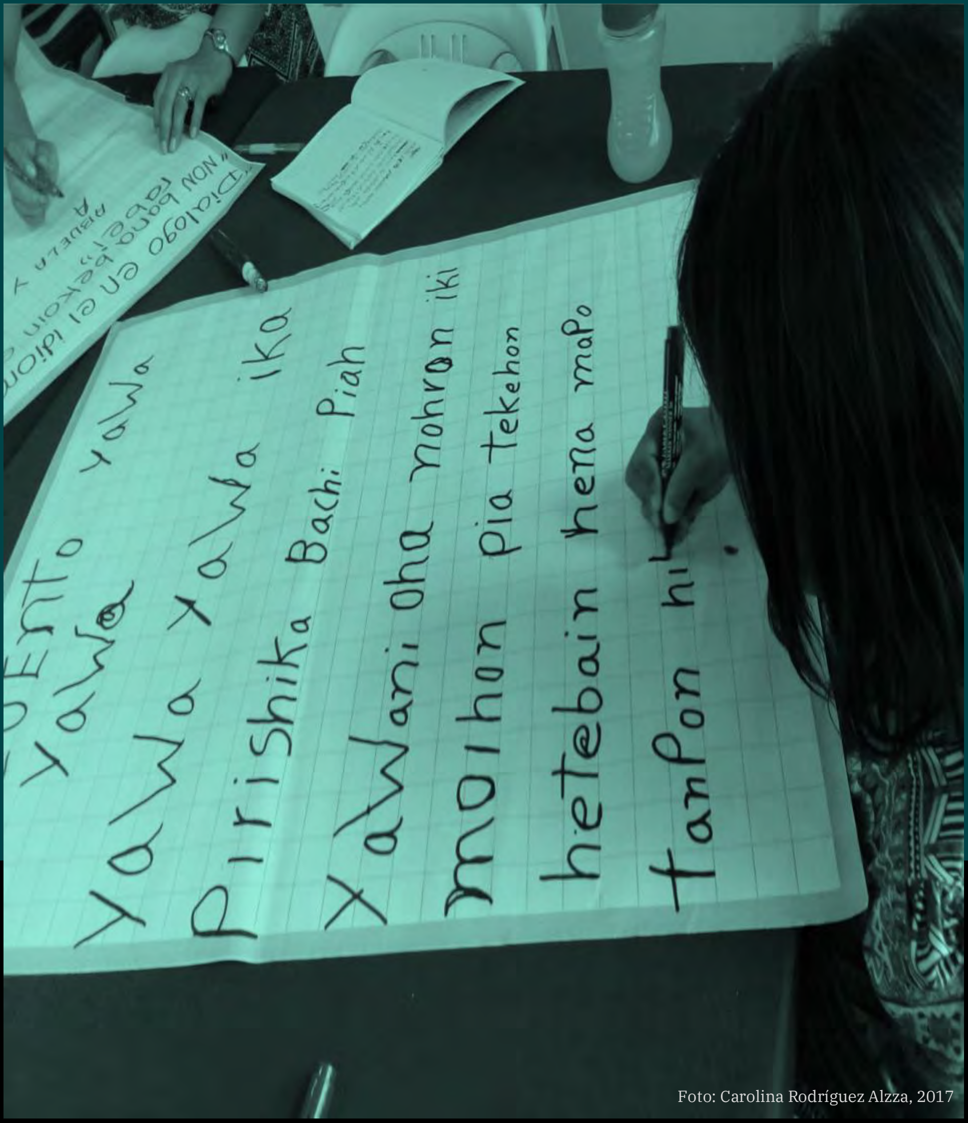

Foto: Carolina Rodríguez Alzza, 2017

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Graphical Abstract

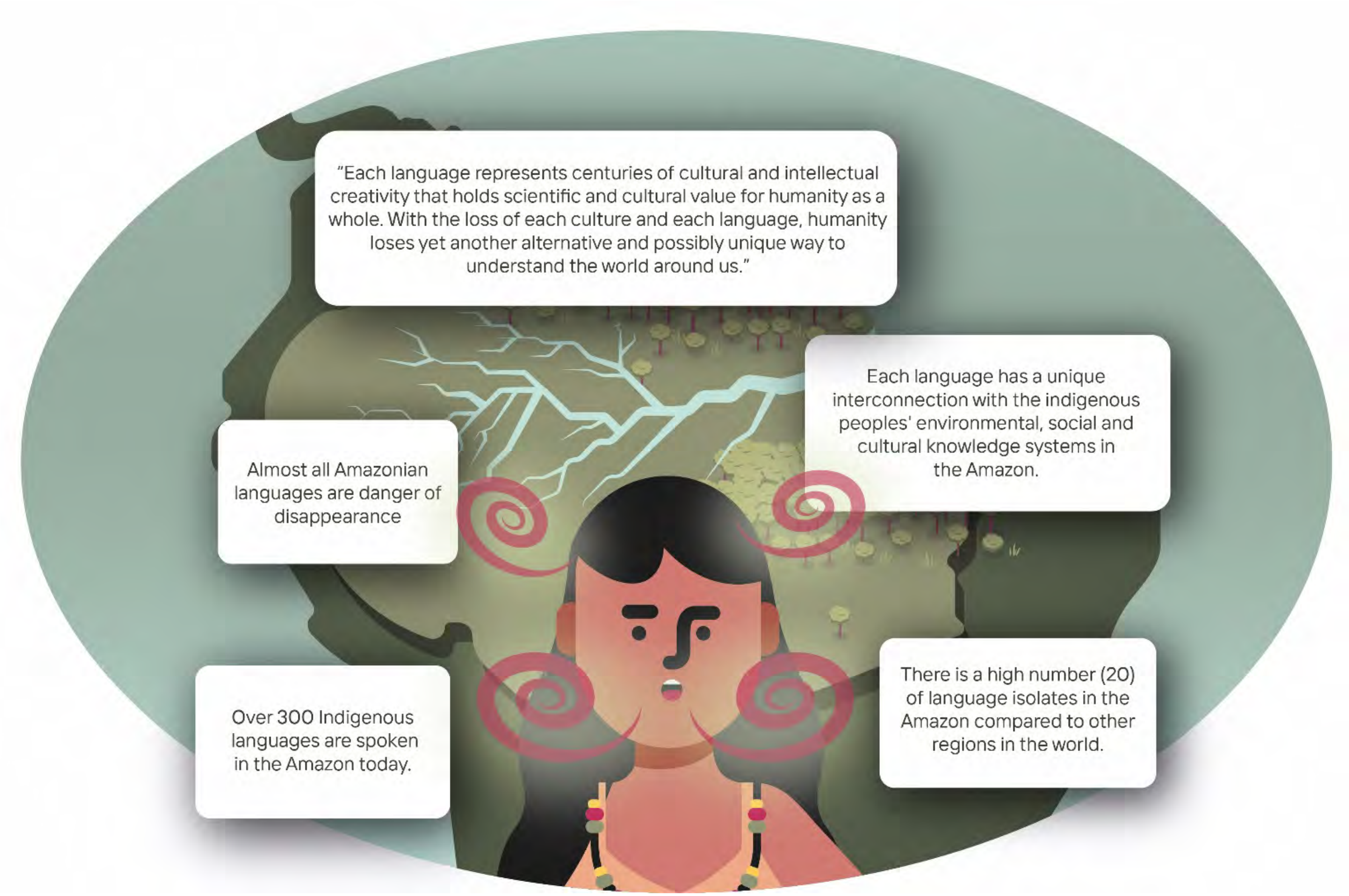

Figure 12.A Graphical Abstract

Languages of the Amazon: Dimensions of Diversity

Hein van der Voort[a]*, *Carolina Rodríguez Alzza*[b]*, *Tod Dillon Swanson*[c], *Mily Crevels*[d]

Key Messages

- One of the most important dimensions of the linguistic diversity of the Amazon region is its genealogical diversity. With respect to language families and isolates, the Amazon is one of the richest parts of the world, and this diversity is, possibly not coincidentally, mirrored by Amazonian biodiversity. Most Amazonian languages are in danger of extinction, whereas few have been sufficiently documented and studied.
- Each language represents the heritage of centuries of cultural and intellectual creativity that holds scientific and cultural value for humanity as a whole. With the loss of each culture and each language, we lose an alternative and possibly unique way, developed over many centuries, of understanding the world.
- All languages and cultures are permanently subject to change, and all are capable of adapting to new circumstances. However, since the arrival of Europeans five centuries ago, the Amazon region has lost 75% of its languages (Aikhenvald 2012, Rodrigues 1993). The disappearance of linguistic diversity in the Amazon, disintegration of Indigenous societies, extinction of biological species, and destruction of Amazonian ecosystems are parts of the same problem.
- Important components of preventing language extinction are valorization of speakers through the recognition of Indigenous rights, the protection of Indigenous lands, and sustainable economic alternatives to uncontrolled deforestation and mineral prospecting. The active promotion of language rights by governments of Amazonian countries is a relevant measure to decelerate their loss.
- Indigenous peoples themselves are taking advantage of growing connectivity throughout the Amazon and are developing solutions by using language in new ways, such as social media, in which young speakers participate without feeling stigmatized and promote documentation and revitalization of their languages.

Abstract

This chapter is about the extraordinary Indigenous linguistic diversity of the Amazon region. This diversity is presented in terms of its different dimensions: the existence of a relatively large number of languages in the region; how these languages are related among each other, representing an impressive genealogical diversity; its geographical distribution over different Amazonian subregions; the effects of language contact that have resulted in several linguistic areas; the different levels of endangerment and the different social circumstances that contribute to it; and, finally, what is lost when languages disappear. The loss of linguistic diversity entails the disappearance of Indigenous knowledge systems concerning environment and social organization, and parallels biodiversity loss.

Keywords: Amazonian languages, language diversity, language vitality, endangered languages, drivers of change

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12.1 Introduction

This chapter presents the dimensions that make the Amazon region a place of extraordinary linguistic diversity. The first reports by European colonizers, missionaries, travelers, adventurers, and scientists mentioned the remarkable multitude of languages spoken by the various peoples of the region. They also highlighted the fact that these languages seemed to be radically different from each other. The number of languages that were spoken at that time far exceeds the over 300 languages that are counted today. These remaining languages are classified in around 50 language families and isolates, resembling a patchwork quilt when indicated by colors on a map (Figure 12.1).

Linguistic research has increasingly refined our understanding of this diversity, not only with respect to genealogical classification, traces of contact, and typological characteristics. Languages also differ due to historical, social, and cultural factors. Furthermore, at the present juncture, languages differ conspicuously with regard to levels of vitality. While some languages enjoy a high degree of vitality and may have the support of national and local language policies, others are at serious risk of extinction. Nevertheless, all Amazonian languages can be considered in some degree of danger, due to the pressures of national and global societies. The ongoing loss of linguistic diversity involves the disappearance of Indigenous knowledge systems concerning environment and social organization, and parallels biodiversity loss.

12.2 Linguistic diversity

In spite of difficulty in establishing the exact number of different languages spoken on the planet, linguists agree that it is at least 6,000. Some of those languages have hundreds of millions of speakers and 20 of those languages are spoken by about half the world's population. This implies that all other languages are spoken by the other half of humanity. It is furthermore estimated that half of the world's more than 6,000 languages are spoken by not more than 0.2% of the world's population. Most of these languages are to some degree endangered (Moseley ed. 2010).

The density of languages is not distributed evenly across the globe. In some regions few languages are spoken, and in other regions the number of different languages is extreme. As an example, one single Inuit language is spoken, in several different dialects, along the coast of Greenland, down from the northwest, rounding the southern tip, up to the east, covering a stretch of 4,000 kilometers. By contrast, in New Guinea, which is about half the size of Greenland, an estimated 1,000 different languages are spoken. In terms of language numbers, New Guinea is extremely diverse.

The Amazon region is also highly linguistically diverse in quantitative terms. It is estimated that over 300 Indigenous languages are spoken in the Amazon today. This number, however, is a fraction of the over 1,000 languages that were spoken when European colonizers arrived. Over the past five centuries, exogenous diseases, colonial violence, slavery, and dispossession have diminished Indigenous populations, and in the process many languages became extinct. Even though Indigenous populations have been rising for the past 50 years, most of their languages are in danger of extinction.

In order to establish what is lost when languages disappear and what are the causes of this process, we will have to explain the nature of language diversity in the Amazon and where it comes from. In the above paragraphs, we have considered language diversity in terms of numbers of languages. There are also other ways to look at language diversity, which are related to the way in which languages emerge and die out again.

12.3 The emergence of genealogical language diversity

All living languages change over time and therefore show variation. Language change can be caused by different internal and external factors.

Languages change through time, which is why we may have difficulty understanding earlier stages of a language as laid down in written form from centuries ago, or sometimes even as spoken by our grandparents. Furthermore, when different populations speaking the same language live separately in distant geographical locations, separate linguistic developments through time give rise to contemporary variations of the same language, known as dialects. If enough time passes, say, a thousand years, dialects may become so different as to no longer be mutually intelligible, and can be considered different languages. Because such languages originate from a common ancestor, they are considered genealogically related.

The emergence of new dialects and languages through historical diversification results in language families. A well-known example is the Romance language family, which consists of Spanish, French, Portuguese, Italian, and other languages, and which developed out of an earlier language known as Vulgar Latin. In fact, the Romance languages are part of just one branch of a bigger and older family, the Indo-European languages, which includes Celtic, Germanic, Slavic, Indo-Iranian, and other language families. The hundreds of Indo-European languages are therefore all genealogically related. There are several very big language families in the world, such as the Austronesian family, the Niger-Congo family, and the Sino-Tibetan family. Three big language families are widely represented in the Amazon region: Arawakan, Cariban, and Tupian.

There are perhaps 250 different language families in the world today, some of which are very small, containing only two or three languages, many of which are found only in South America. Some languages are isolates; they do not belong to any known family and can be considered as single-language families. A European example is Basque, which even after centuries of linguistic research has not been classified in any known family (but see Bakker 2020). There are about 125 isolates in the world, and the Amazon region harbors a disproportionate number of those (Seifart and Hammarström 2018). To explain this high number of isolates represents a challenge for Amazonian linguistics and related areas of research.

Table 12.1[1]shows that the Amazon region has a relatively low number of languages when compared to some other regions. However, the number of families and isolates represented by those relatively few languages is very high. In terms of genealogical units, the linguistic diversity of the Amazon is quite exceptional.

Table 12.2[2] looks more in-depth at this diversity, considering each country in the Amazon basin. The numbers shown are rough approximations. Most of

Table 12.1 Some indicators of linguistic diversity[1]

	Languages	Families	Isolates
World	6,000+	250	125
North America	400	35	20
South America	500	45	40
Amazon	300+	25	20
New Guinea	1,000+	50	20

Table 12.2 Number of languages, families and isolates in the Amazon[2]

Country/territory	Languages	Families	Isolates
Brazil	120	14	7
Bolivia	34	11	8
Colombia	49	13	6
Ecuador	9	4	2
French Guiana	6	3	-
Peru	48	19	5
Venezuela	37	5	4

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[1] Based on Moseley (ed. 2010), Hammarström et al. (2021), Campbell (ed. 2018) and other general resources

[2] Based on Crevels (2012) and Moore (2007).

the languages belong to one of the major linguistic families (Tupi, Arawak, Carib, Macro-Jê). The literature on these families is vast. For general overviews see, e.g., Campbell and Grondona eds. (2012), Dixon and Aikhenvald eds. (1999), Epps and Michael eds. (in prep).

The classification of languages into families requires careful historical comparative linguistic research and depends on reliable and well-analyzed descriptive linguistic data. Especially in the Amazon, such data are not always available, and in view of the endangered situation of most Amazonian languages, researchers face a race against time. The scientific relevance of the genealogical linguistic diversity of the Amazon has ramifications for other fields of science, such as archaeology.

The geographical distribution of language families can be shown on a map by using different colors and can help to reconstruct patterns of prehistoric demography and migrations. Figure 12.1 shows the linguistic diversity of the Amazon.

Furthermore, the greater the diversity within a language family in a specific region, the more likely it is that language family originated there. Hence, the center of origin of the Tupi language family is estimated to be in the border region of the Brazilian states of Mato Grosso and Rondônia (Galucio *et al.* 2015). Classification of languages involves the reconstruction of sound changes and words, such as terms for material and immaterial culture, subsistence technology, and features of nature and the landscape. Hence comparative linguistics can teach us not only about where people lived but also about how they lived (Campbell 1998).

Comparative linguistics also involves establishing relative time depth between languages of the same family. The historical comparative method can look back in time perhaps up to 7,000 years. Beyond that, languages may have changed so much that it is not possible to establish any family relationship. This is also one of the factors that can explain the existence of language isolates. Another possible explanation of isolates is that all other languages of the same family have died out.

With over 10 language isolates on the headwaters of the Guaporé and Mamoré rivers, a region the size of Germany, the southwestern Ama-zon harbors one of the greatest concentrations of linguistic isolates on the planet.

By definition, language isolates do not share a common ancestor with any other known languages and are thus genealogically unique. Consequently, their vocabularies tend to be completely different and they may display structural properties that have never been attested for any other language. On the other hand, the fact that any language, including isolates, also shares properties with other languages may also be the result of language contact, or may point to traits, tendencies, or limits that are universal in human language. Therefore, the research of grammatical structures of all languages is not only relevant for the typological study of language, but may also have great significance for the study of cognition and the human brain.

12.4 Language diversification and change through contact

Languages can change through contact with other languages. Language contact occurs in situations of bi- or multilingualism, or when people who do not speak each other's language are in contact (Thomason 2001; Winford 2003). Prime indicators of language contact are loanwords, but languages can also undergo influence in their sound systems and grammar. Due to contact, languages can display specific similarities with other languages even though they are not genealogically related. One of the challenges of comparative linguistics lies in distinguishing the contact signal from the genealogical signal (Campbell 1998). Vestiges of language contact and knowledge about the directionality of linguistic influence can be highly relevant for our understanding of present and past cultural, societal, and trade relationships between populations.

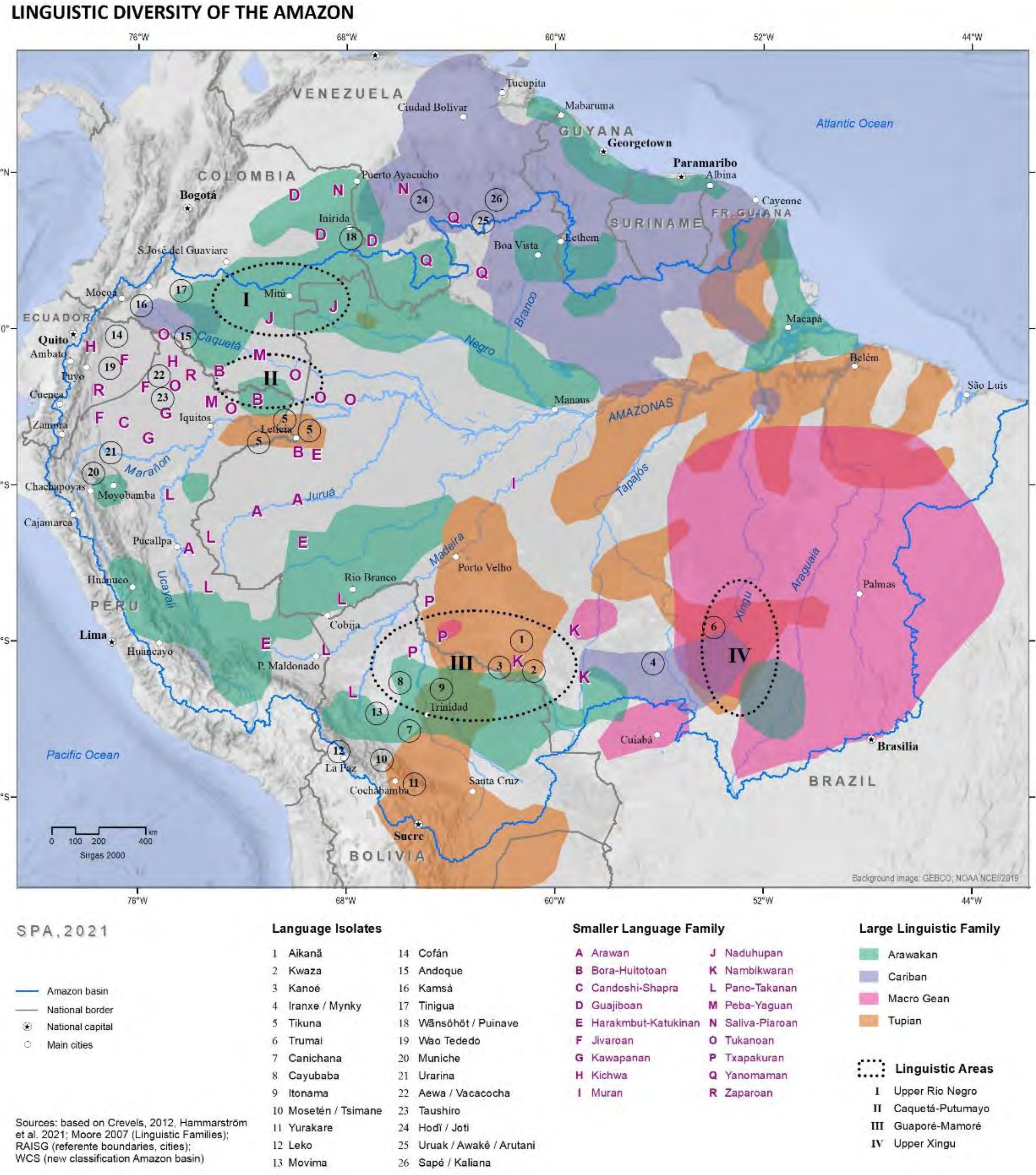

Figure 12.1 Linguistic diversity of the Amazon. Sources: Crevels (2012), Hammarström *et al.* (2021), Moore (2007), RAISG (2020), Venticinque *et al.* (2016).

Language contact can lead to the emergence of new languages. When different groups do not understand each other's languages, they may create a grammatically simplified language with a limited vocabulary, known as a *pidgin*. Pidgin languages are not spoken as a mother tongue and are used in specific contexts, such as for the purpose of trade. In more profound or dramatic situations of intercultural contact, a pidgin language may be the only language available to the new generation and result in a new language that is spoken as a first language. In the context of the Atlantic slave trade many *creole* languages have emerged; these are languages with a lexicon that tends to originate from the dominant languages involved in the contact and a grammar that cannot be traced back to any specific language, but that may reflect universal traits. An Amazonian example of a creole language is Kheuól, which is based on French lexicon and spoken by the Karipuna do Amapá and the Galibi-Marworno Indigenous peoples (Ferreira and Alleyne 2007).

Another type of new language is an *intertwined* or *bilingual mixed language*. Such a language may arise under rare social circumstances when a new ethnic group emerges out of two different ethnic groups and feels the need to have a language of its own. Such mixed languages tend to be composed of the grammatical and lexical components of the contributing languages. A South American Indigenous example is Island Carib, which is a language with Arawak grammatical structure and Carib lexicon that emerged when Carib speaking men massacred the men of an Arawak speaking group and married their women. Their children acquired the grammar from their mothers and the lexicon from their fathers (Hoff 1994).

Pidgins, creoles, and mixed languages cannot be satisfactorily classified in families, because they do not have a clear single ancestor. Creoles and mixed languages are very rare in the Amazon region. However, such languages are spoken natively and undergo processes of linguistic change through time like any other language. Therefore, the possibility cannot be excluded that certain known Amazonian language families or isolates started out as creoles or mixed languages many centuries ago. There exists hardly any documentation and research of Indigenous Amazonian pidgin languages. One explanation for the relative absence of contact-induced new languages in the Amazon combines the enormous language diversity of certain regions with widespread traditions of multilingualism.

Situations of long-term language contact and multilingualism in a specific region can result in the diffusion of lexical, phonological, and grammatical traits among languages irrespective of their genealogical classification (Hickey ed. 2017; Matras *et al.* 2006; Muysken ed. 2008). Over time, say, several centuries, the languages involved may come to resemble each other and form a so-called *linguistic area* or *Sprachbund*. A classic example is the Balkans region, where the Slavic, Albanian, Rumanian, Turkish, Romani, and Greek languages have certain traits in common that are unknown among other Slavic, Romance, and Turkic languages outside the region. The Amazon region contains several linguistic areas (indicated in dotted circles in Figure 12.1). The most famous and striking is the Upper Rio Negro region where the Tucanoan, Arawakan, Naduhup, and Kakua-Nukak languages share grammatical traits that are not shared with genealogically related languages outside of the region (Aikhenvald 2002; Epps and Stenzel eds. 2013; Epps and Michael 2017).

12.5 Language variation

Both historical language change and contact-induced language change are kinds of linguistic variation. In fact, variability is an important characteristic of any language. What is usually called a "language" is not a clearly definable entity. A living language may vary through time; by region; across social strata; according to occupation, gender, or age; depending on audience; etc. The documentation and description of widely-spoken European languages, such as Spanish, English, or German, covers hundreds of years of social, regional, and other kinds of variation. The study of these languages occupies large portions of archives and libraries, and results in many new books and digital projects each year. The contrast with Amazonian languages could not be greater. We are lucky if an Amazonian language can boast of a single comprehensive grammatical description, and many Amazonian languages are underdocumented. Nevertheless, Amazonian languages are as rich and variable as any other language, and fortunately the documentation and study of dialectal variation, speech styles, specialized language use, and verbal art are beginning to receive the attention they deserve (e.g. Beier *et al.* 2002; Hildebrandt *et al.* 2017).

Concrete examples include the Hup (Naduhup) language of the Brazilian-Colombian border, which has three dialect areas where pronunciation, the meaning of words, and grammar may differ. The Mondé (Tupian) languages of the Zoro, Cinta Larga, Gavião, and Aruá ethnic groups of Brazil are in fact different dialects of the same language. They are mutually intelligible, even though each group may insist that the other group "speaks differently". Several Amazonian languages have separate speech varieties for men and women. In Kukama-Kukamiria (possibly creolized Tupi-Guaranian) of Peru and Colombia, for example, men and women use different personal pronouns. Many Indigenous groups, for example the Yanomami of Brazil and Venezuela, the Kalapalo (Cariban) of Brazil, and the Nanti (Arawakan) of Peru, perform ceremonial dialogues in greeting rituals, storytelling, news reports, and other special occasions. These are just a few examples of language variation in the Amazon region. One of the first signs of language endangerment is the loss of such variation. The further a population shifts to another language, or the more its social customs are under outside pressure, the less possibilities and opportunities there will be for dialectal, social, or other variation in the original language.

12.6 Language vitality and endangerment

As mentioned above, many Amazonian languages have become extinct during the past few centuries. Languages can become obsolete and disappear in different ways. This may happen when languages change in a gradual historical process. Alternatively, people may abandon their native language and switch to another existing language, usually for economic, political, or other reasons. Languages may also become extinct when their speakers die out, for example due to natural disasters or genocide.

The emergence and extinction of languages can be regarded as a natural process that has always existed. However, since the onset European colonization in the 15th century the cycle has been definitively broken and many more languages are becoming extinct than new languages emerge. During the last century, this process has even accelerated. This has led to a dramatic decline of language diversity and of the immaterial cultural and historical heritage contained in it.

Nevertheless, many languages in the Amazon Basin survive today. Up to 200 isolated or recently contacted Indigenous groups (IACHR 2013; Loebens and Neves eds. 2011; Ricardo and Gongora eds. 2019) continue to speak their languages. Amazonian Indigenous groups struggle to maintain their languages inside as well as outside of their own territories. In cities, for example, the national language is dominant and the use of Indigenous languages is often stigmatized. The development of language policies may counteract prejudice and support the use of Indigenous languages as a fundamental right. Such policies can encourage people to speak their local language. However, socioeconomic factors may diminish the impact of such policies.

There are different proposals to measure the degree of language endangerment or vitality (Wurm ed. 1996; Krauss 2007; Brenzinger 2007; Moseley 2009; Lewis and Simons 2010; Campbell 2017; Hammarström *et al.* 2018; Lee and Van Way 2018). Most of them have created categories for different

Table 12.3 Evaluative factors for language vitality (UNESCO 2003)

Factor	Characteristic
1	Intergenerational language transmission
2	Absolute number of speakers
3	Proportion of speakers within the total population
4	Shifts in domains of language use
5	Response to new domains and media
6	Availability of materials for language education and literacy
7	Governmental and institutional language attitudes and policies including official status and use
8	Community members' attitudes towards their own language
9	Type and quality of documentation

Table 12.4 Proportional representation (5%) of the endangerment situation of Amazonian languages (partially adapted from Crevels 2012)

LANGUAGE	FAMILY	COUNTRY	POPULATION	SPEAKERS	DANGER LEVEL
Cayubaba	ISOLATE	BO	1,424	< 2	critical
Záparo	ZAPAROAN	EC	346	2	
Kanoé	ISOLATE	BR	310	4	
Akuriyo	CARIBAN	SU	50	3	
Latundê	NAMBIKWARAN	BR	22	18	severe
Pisamira	TUKANOAN	CO	61	25	
Lokono	ARAWAKAN	GY/GF/VE/SU	19,500	2,500	
Miraña	WITOTOAN	CO	715	<100	
Machiguenga	ARAWAKAN	PE	11,238	5,000	endangered
Cavineña	TACANAN	BO	2,005	601	
Rikbaktsa	MACRO-JEAN	BR	1,323	1,085	
Shiwiar	JIVAROAN	EC	1,198	942	
Emérillon	TUPIAN	GF	400	400	
Kuiva	GUAHIBOAN	CO/VE	1,840	1,840	
Matsés	PANOAN	PE/BR	6,500	6,500	
Tikuna	ISOLATE	BR/CO/PE	50,000	50,000	relatively safe

degrees of endangerment, such as vital, vulnerable, in serious danger, and critically endangered.

The assessment of endangerment for each of the 2,464 languages included in the UNESCO *Atlas of the world's endangered languages* (Moseley ed. 2010) has been based on nine evaluative factors of linguistic vitality. These factors, listed in Table 12.3, were established by an UNESCO (2003) ad hoc expert group of linguists.

The number of speakers (Factor 2) and their proportion with respect to the total population (Factor 3), are important criteria for evaluating language vitality. Unfortunately, these numbers are often not clearly specified, which may lead to confusion and unreliable figures as observed by Moore (2007). The Yawalapiti people of Brazil comprise 262 individuals, whereas the Ocaina people of Peru number only 150. However, the Yawalapiti language has at most 5 speakers (Troncarelli and Viveiros de Castro 2021), whereas about 50 persons speak the Ocaina language (Crevels 2012). This means that only 2% of the Yawalapiti population speak the language, whereas 33% of the Ocaina population speak the language.

Besides speaker numbers, the evaluation of language vitality must also include other factors. Transmission of a language between generations (Factor 1) is a crucial component. A language with a thousand speakers is not necessarily a vital language if its speakers are limited to older generations, with few or no young speakers. Interruptions in transmission to the next generation usually results from chronic oppression of Indigenous populations and stigmatization of their languages. One consequence of a break with the linguistic heritage is the loss of the oldest speakers' historical, social, cultural, and environmental knowledge. Some of the reasons that younger generations prefer to learn major national languages over Indigenous languages will be discussed in the sections below.

All Amazonian languages are threatened with extinction in one way or another. Perhaps only 20 of the over 300 Amazonian languages can be considered relatively safe in terms of the degrees of endangerment distinguished by UNESCO (see Moseley 2012). About 150 languages are endangered (ranging from vulnerable to definitely endangered), around 75 are seriously endangered, and no less than 75 are critically endangered. Table 12.4 is intended as an illustrative sample of 16 Amazonian languages proportionally distributed over the different degrees of endangerment.

Amazonian populations have always been part of extensive social networks. Coexistence and sharing of social activities; such as rituals, festivities, and intermarriage; have encouraged people to learn more than one language. The Colombian "People of the Center" represent a cultural complex in which seven ethnolinguistic groups converge, speaking different languages from three linguistic families, and one isolate: Murui-Muina, Ocaina and Nonuya (Witotoan), Bora-Miraña, Muinane (Boran), Resígaro (Ara-wakan), and Andoque (isolate). Despite the linguistic differences, communication is possible thanks to a common socio-cultural background underlying the oral traditions (mythical heroes, similar discursive genres). In healing ceremonies or festivals, for example, each community uses its own language; the success of communication lies in mutual knowledge, active or passive, partially supported by inter-ethnic marriages and alliances. Increasing contact with Western society has also motivated people to learn national languages, such as Spanish or Portuguese. Nevertheless, part of the population is still monolingual in an Indigenous language, especially those belonging to older generations. Young people and adults are often bilingual or even multilingual.

Despite the multilingualism that characterizes many Amazonian populations, Indigenous languages are progressively used in fewer domains (Factor 4). Depending on the particular context, this can be due to a language ideology that associates Indigenous languages with a low educational level, poverty, or rurality, and national languages with social, cultural, and economic development. This fosters discrimination and shaming of local language speakers, leading them to avoid speaking their language in public, for example. Furthermore, the dominant linguistic domains of work opportunities and socioeconomic advancement motivate the shift to a national or global language. For either of these reasons, speaking one or several Indigenous languages is not seen as an advantage (Factor 8), and those languages may lose domains of use.

In spite of such adverse tendencies and attitudes, Indigenous peoples themselves are increasingly concerned about the predicament of their languages, and are demanding effective policies to protect their linguistic rights. It is a hopeful development that they are organizing on national and international levels to stem the tide of language loss. Indigenous peoples are now taking the lead in initiatives, such as the Latin American Work Group that aims to develop strategies within the framework of the United Nations proclamation of 2022-2032 as the International Decade of Indigenous Languages.

12.7 Official policies supporting language maintenance

Governments tend to have different policies, depending on whether they consider language diversity as a problem or as a right (Factor 7). In Bolivia, Indigenous languages are officially recognized at the national level through Article 2 of the Constitution. Likewise, according to the Peruvian and Colombian Constitutions, languages are officially recognized in the territories where they are spoken. Other countries, such as Ecuador and Venezuela, state in their Constitutions that Indigenous languages are official for the groups who speak them. Only Bolivia requires the use of at least two languages in its government activities by law. While one of them must be Spanish, the other can be an Indigenous language according to convenience. In other Amazonian countries, the use of Indigenous languages is officially recognized only where they are predominant. In the Brazilian municipality of São Gabriel da Cachoeira, the Nheengatú, Baniwa, and Tukano languages have co-official status.

As Table 12.5 shows, some Amazonian countries have developed additional laws with regard to Indigenous languages. Brazil includes the constitutional right to maintain native languages and has a language policy in its education law. In recent years, Ecuador opened a debate around the relevance of having a national language policy. Furthermore, Indigenous organizations around the Amazon have undertaken initiatives to further the recognition of their languages as part of Indigenous rights.

In Peru, the Autonomous Territorial Government of the Wampis Nations declared the necessity of continuing to transmit the Wampis language and to guarantee education in it. Despite such advances,

Table 12.5 Selected laws with regard to Indigenous languages

Country	Title	Year
Bolivia	Constitution General law of linguistic rights and policies (N° 269)	2009 2012
Brazil	Constitution Education Guidelines and Bases Law (N° 9.394/96) National Inventory of Linguistic Diversity (N° 7.387/10)	1988 1996 2010
Colombia	Constitution Law of languages (N° 1381)	1991 2010
Ecuador	Constitution	2008
Peru	Constitution Law that regulates the use, preservation, development, recovery, promotion and dissemination of the original languages of the Peru (N° 29735)	1993 2011
Venezuela	Constitution Law of Indigenous languages	1999 2008

Indigenous language speakers continue to face severe difficulties in using their language in public places or when trying to access government services.

Indigenous language teaching at schools is one of the language maintenance strategies that is supported by policies in some countries. Around the mid-20th century, Amazonian states began to develop bilingual education plans with the participation of the evangelical Summer Institute of Linguistics (SIL). After official agreements with the states and education ministries, SIL missionary linguists were deployed throughout several countries and established bases close to Indigenous lands. One of their methods was the placement of Indigenous teachers in order to open schools in communities and to start teaching in their own language as well as in the national one. Later, the educational sectors of Amazonian countries assumed responsibility for Indigenous education and the creation of pedagogical materials. For example, in Ecuador a bilingual intercultural education system (DNEIB) was created in 1988. The Peruvian government has proposed to extend bilingual intercultural education to high schools in its plan towards 2021.

Governments often lack detailed knowledge about minority languages spoken in their countries. Especially with regard to Indigenous languages, access to reliable information is difficult, if it is available at all. When the Brazilian government realized that its high linguistic diversity represented intangible cultural heritage it decided to develop a policy towards protection. This resulted in an initiative to set up a National Inventory of Linguistic Diversity. With the help of professional linguists, pilot projects have now been initiated with a number of languages, aiming to collect basic linguistic and ethnohistorical information, detailed knowledge of the actual sociolinguistic situation of each language, and of speakers' demands for language protection and revitalization (see Galucio *et al.* 2018). The ultimate goal of a complete inventory will be a solid basis for informed governmental language policies.

12.8 Documentation

All Amazonian languages continue to be endangered to some degree. Therefore, professional language documentation and description are of utmost importance (Factor 9). A language description should consist at least of a comprehensive grammar, dictionary, and collection of texts. In the 1990s, international alarm about the global language extinction crisis caused linguists to step up efforts to document languages. By the turn of the century, documentation had become a subdiscipline of linguistics. This was furthermore encouraged by the digital revolution that created the internet and that enabled high-quality audiovisual registration, using highly portable field equipment available at relatively low cost. Modern linguistic documentation consists of creating a comprehensive, permanent archival record of a language as used in different social and cultural contexts, representing as wide as possible a range of different varieties and types of discourse (Gippert *et al.* 2006; Woodbury 2003). During the past decades, various local and international language and culture documentation programs have supported projects in the Amazon, and a considerable number of languages possess substantial audiovisual records in properly catalogued online digital archives in Europe, the United States, and Brazil. Such material can be used as the basis for pedagogical material and has the potential to feed language revitalization efforts. Some of the complex issues involved in Indigenous language archives include online accessibility, differential rights to usage, and questions of privacy (Seyfeddinipur *et al.* 2019). In spite of these developments, the majority of Amazonian languages still lack adequate description and documentation, whereas this is often one of the principal demands of Indigenous groups with regard to language (Galucio *et al.* 2018). As experience shows, documentation tends to be desperately sought after a language has disappeared. One of the possible solutions would be to create regional documentation centers and language archives, where Indigenous peoples can develop their own documentation initiatives.

12.9 Drivers of change: Some examples

Although change is natural, the Amazon region is losing linguistic diversity at an alarming and accelerating rate. To understand how the drivers of this change operate it is useful to recall that language vitality requires a critical mass of speakers living in the same area, and that this population must have confidence that their language has a future, and that it will be a productive medium of their children's livelihood and as well as their social well-being. Drivers of change are factors that may threaten these conditions.

Christian missionary movements, epidemics, and a succession of extraction booms (*cascarilla*, quinine, rubber, wild animal skins, petroleum, and mining) have been major drivers of language loss. Three religious movements in particular stand out for the extent of their impact: the Catholic Jesuits (1600-1767), the Catholic Salesians (1880-present), and the Protestant Summer Institute of Linguistics / Wycliffe Bible Translators (1945-1970). Despite differences, these groups are similar in that they had well developed language policies, pan-Amazonian strategies, functioned as (quasi-)government institutions, and were motivated by Christian zeal. Significantly, the Jesuits and the Summer Institute were also eventually expelled from the region because their sway over the native population exceeded or rivaled that of the state.

In 1668, Bishop Alonzo de la Peña Montenegro established a language policy for missionary priests working throughout the Kingdom of Quito, which at that time included all Spanish claims in the Amazon, in a massive work entitled *Itinerario para Parrachos de Indios*. Although his writings most directly concern what is now Ecuador and Peru, they had implications for the broader region under his jurisdiction. In this work the bishop ruled that all missionary priests must learn an Indigenous language (De La Peña Montenegro 1668: 21). At the same time, he recognized that in some missions there were too many languages for a single priest to learn. He cites San Jose de Avila on a tributary of the Río Napo where eight different languages were spoken. Since it would be impossible to learn all of these, he ruled that a regional language should be selected and taught to the speakers of smaller languages (De La Peña Montenegro 1668: 32).

The Jesuits' selection of which language to use was based in part on a moral hierarchy grounded in their beliefs about the origins of linguistic diversity. According to Father Bernardo Recio, a first division into 60 primary languages "was ordered by God Our Lord for the good of the human race" at the tower of Babel. These languages correspond to the agrarian civilizations organized into villages governed by reason and natural law which the Jesuits sought to create in their reductions as precursors to a converted Christian society. One of these languages, according to Recio, is the "language of the Inca" which in the dialect of Quito is called "Quichua". Quichua, he writes, "is genuinely, and of itself a language, and as a root and fount of many languages one may suppose that it was among the sixty-two of the tower of Babel" (Recio [1773] 1947: 413-414)[3]. Although Kichwa was only the language of missions in certain areas of the western Amazon, Recio's exalted opinion of this language is indicative of broader Jesuit attitudes toward the trade languages they selected. By contrast, what Recio calls "the very strange division of the gentile languages" into those spoken by the smaller groups of Amazonian peoples, were not, in his opinion, the work of God, but rather degenerations inspired by the devil, or as he put it, that "enemy of the human race to make the remedy of their health [the preaching of the gospel] more difficult and even impossible" (Recio [1773] 1947: 465) As such, these languages were not believed to be capable of rational, civilized, or moral communication and were not to be preserved. It was morally permissible to capture the speakers of these languages "for their own good" and teach them the rational and moral language of the mission.

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[3] "Quichua" is the colonial spelling used by Recio for the language now officially written as "Kichwa" in Ecuador.

Indigenous Amazonians did not, of course, change languages just to please the Jesuits. The process was complex. Missionary journals from this period portray a region undergoing great mobility, with speakers of one language often moving into the territory of another group to escape epidemics or slave raiders, sometimes displacing groups who had lived there earlier. Population collapse combined with mobility likely led to marriage between people who spoke separate, smaller languages but shared a trade language in common. Although data is limited it seems clear that the colonial disruption of the Jesuit period led to the loss of many smaller languages. Of the eight languages Peña Montenegro knew were present at the seventeenth century mission of Avila, only Kichwa remained by the nineteenth century. In all of this the Jesuit mission infrastructure played a role in determining which languages survived and came to be seen as more civilized or Christian languages. It is important to note that the beneficiary of this reduction of diversity was not Spanish or Portuguese, but rather regional native trade languages as well as an increase in bilingual ability in these languages. In 1767 the Jesuits were expelled from the Spanish and Portuguese colonies and the missions fell into neglect.

In the 1880s, the rubber boom, which affected so many other aspects of Amazonian life, had a major impact, resulting in the expansion of some languages and the extinction or isolation of many others. International demand for rubber promoted an increasing Indigenous labor force. Many Indigenous people were congregated in rubber settlements where they lived in a precarious situation of overcrowding and poor sanitation. The foremen raided Indigenous communities and kidnapped young people who grew up working on the rubber settlements. Other Indigenous people came to the rubber factories through schemes of indebtedness variously called *habilitación*, *repartos*, or *endeude*. This consisted of a debt that could never be paid off. Tired of the violent treatment, many Indigenous people fled to the forest and became isolated again. Other Indigenous people died from the precarious conditions in which they lived and physical violence. In this way Indigenous people, fratrias, moieties, and clans were decimated or physically eliminated (e.g. the Nonuya and Tinigua in Colombia), thus compromising the system of marriage alliances and the transmission of languages.

Although the Jesuits had been expelled, other Catholic missions continued, sometimes with devastating effects on Indigenous cultures and societies. By the end of the 19th century, mission villages were established in the Rio Negro region. Local Indigenous groups fleeing abuse in rubber settlements were enticed or forced to relocate to missions, where they were forbidden to maintain their religious and cultural traditions. Based on published sources such as Nimuendajú (1950) and Hemming (2003) as well as on personal interviews, Epps (2005) relates how the Salesian missions gained increasing control of the region during the first half of the 20th century. One of the first strategies used to destroy Indigenous lifestyles was to eradicate communal houses, demonizing those as dirty, promiscuous, and infernal. They furthermore campaigned to ridicule and defame shamanic practices and actively destroyed ritual objects and ceremonial musical instruments. They replaced Indigenous traditions with Catholic rituals and doctrines. Initially, the Salesians approached Indigenous languages with disdain, but later saw that the use of a local language would be advantageous, promoting the Tukano language, which then gained prestige and dominance in the region. One of the most devastating and well-tried tactics used against Indigenous language and culture were mission boarding schools, where younger generations were alienated from their families and culture, received corporal punishment for speaking their native language, and were indoctrinated with mission culture and religion (Epps 2005).

As the twentieth century progressed, a significant driver of linguistic and cultural change was the accelerating connectivity of the previously-isolated whitewater regions, such as the headwaters of tributaries in the western Amazon where the greatest concentration of language families and language isolates lie. In the absence of roads and airstrips, the rugged geography of these areas had created refuge zones limiting contact not only with the state but also between Indigenous languages. Developments around World War II began to break this isolation. In the 1930s, to meet the heightened demands for the war, Standard Oil in Peru and Royal Dutch Shell in Ecuador built roads and airstrips to facilitate extraction in the heart of areas where uncontacted groups lived. A similar dynamic occurred in other countries. The need for Indigenous labor in these industries brought previously isolated groups speaking Indigenous languages into a common workforce.

In the period immediately following World War II, the Summer Institute of Linguistics (SIL or ILV by its acronym in Spanish) formed contracts with ministries of education in various Amazonian countries (Peru 1945, Ecuador 1952, Bolivia 1955, Brazil 1956, Colombia 1962, Surinam 1967) (CEAS 1979). Their mission was to systematically develop orthographies for every Amazonian language, translate the Bible into each of these languages, and teach Indigenous peoples to read them. To do so they created large North American base camps at Yarinacocha in Peru, Limoncocha in Ecuador, Loma Linda in Colombia, Porto Velho in Brazil, and Tumi Chucua in Bolivia. Native consultants from many small languages were brought to live in residence at these bases for the academic year. During the summer months the SIL linguists would then go to live in the consultants' communities. To facilitate travel between the Indigenous group and the base camp they created airstrips in remote locations. This strategy greatly increased communications between language groups at the bases as well as with the state.

SIL's language policy differed from that of the Jesuits in significant ways. Drawing on Martin Luther and John Wycliffe's arguments for translating the Bible into German and English they argued that the Bible could be translated into any language without losing any significant meaning. In practice, this meant that unlike the Jesuits who ascribed higher moral value to regional languages, they saw all languages as morally neutral and interchangeable structures. In fact, they seemed to prioritize the most remote or even the uncontacted Amazonian languages, such as their most famous mission among the Wao Tededo (Waorani) in Ecuador (Long 2019).

Furthermore, the SIL was religiously motivated to create literate readers in each Amazonian language. This meant that they created not only dictionaries and grammars but also native language didactic materials for grades 1-6. They also used their Amazonian bases to train the first bilingual school teachers in many of the Amazonian languages, all this outside the community context. The legacy of the SIL for Indigenous languages was mixed. On the one hand, the visibility and prestige of the smaller languages was raised. The SIL's contracts with ministries of education gave these language groups a more direct contact with the state, likely slowing their assimilation in favor of regional languages. By systematically creating scripts that resembled Spanish and Portuguese they facilitated bilingual integration with Spanish or Portuguese. However, they also left behind a persistent controversy between older scripts, which resemble Iberian languages and scripts, and those adopted by more recent Indigenous movements which stress difference. SIL surveys of Amazonian language diversity increased the number of recognized languages and dialects. They also created the Ethnologue (Eberhard *et al.* 2021), which many rely on for statistics on the variety and vitality of Amazonian languages. At the same time, the SIL is a conservative North American missionary organization dedicated to undermining traditional Indigenous ceremonial practices, declaring them demonic and converting Indigenous groups still living in voluntary isolation. Because these practices were eventually seen as incompatible with serving as an arm of ministries of education in lay states, the SIL lost their contracts across the region by the 1980s. Nevertheless, the SIL continues to represent a key partner in an international network of evangelical organizations that are very active in religious proselytism across the Amazon.

As communication with remote language areas opened up in the first half of the twentieth century, speakers from these smaller languages gradually became more integrated as voting members of the state. Service in the national military brought young men from different language groups into sustained contact with each other and helped to forge a common linguistic identity as, for instance, Peruvians, Brazilians, or Ecuadorians who spoke the language of the state. For young women during this period it was often marriage to a mestizo man or the experience of working as a live-in domestic in a regional town that provided sustained contact with the national language.

In these new contexts, the parents of the contemporary generation often experienced serious language discrimination, causing them to encourage their children to speak Spanish or Portuguese to avoid suffering what they had suffered. The languages of the state are not the only beneficiaries of language discrimination. Accelerating connectivity also created hierarchies between native languages. Smaller, more recently contacted languages were often seen as backward or savage when compared to the larger, more cosmopolitan languages of the missions, such as Kichwa or Língua Geral. As a result, smaller native languages lost speakers to larger native languages and these to the languages of the state.

Perhaps the greatest driver of language loss, however, is a change in the type of employment young people aspire to. Because land loss, deforestation, and the depletion of game animals have made sustaining a family in Indigenous territories more difficult, many seek jobs outside, such as seasonal work in oilfields in Ecuador, or in agriculture. For administrative jobs, formal education is required and although governments throughout the Amazon have committed to providing native language education, serious difficulties remain. For example, many native communities are too small to meet the threshold of the number of children required to make a school economically or administratively viable and there is often a scarcity of qualified teachers willing to serve in remote areas. As a result, many families in Ecuador, Brazil, and elsewhere send their children to regional high schools where the language of instruction is Portuguese or Spanish. As a result, these languages tend to become the preferred means of social communication between teenagers, as well as exemplifying the kind of educated speech most likely to lead to the desired employment. When combined, these linguistic domains represent what many speakers perceive as the language of a good future. The children who attend these high schools speak better Spanish or Portuguese and may get better jobs than do their cousins who remained in their communities without attending high school. Too often, however, the expectation of a better future turns out to be a mirage. Many Indigenous youth who have completed high school are unable to continue further education due to poverty, substandard high schools, discrimination, and a general lack of scholarships. Many become Spanish or Portuguese language dominant without receiving the advantages of employment in the national or global marketplace. As a result, some feel alienated from the urban centers to which they migrate without a viable path for permanent return to their communities of origin.

In contrast to the increasing prestige of global languages, native languages become increasingly associated with domains of use perceived as having a more limited future. For example, girls may associate their native language with being an expert manioc gardener or chicha maker. Men associate their native language with being an expert hunter. Although these skills used to make a person highly desirable, the livelihood they provided has become less sustainable. As a result, increasing numbers of young people aspire to marry someone with a high school or college degree and proficient in the language of professional employment.

12.10 What exactly is being lost? Some examples

What is being lost when languages disappear? That is the topic of a wonderful book by linguist Nicholas Evans (2010). In this section we will only mention a few examples from the Amazon. It is easy to underestimate the extent of language loss because it occurs not only in numbers of speakers, but also less visibly in the functions, domains, and ways in which languages are used. What is actually being lost? The broader work of the SPA examines threats to the biodiversity of the region as a whole. The loss of language diversity is interconnected with environmental destruction and the broader loss of species in the micro-environments where languages are spoken. Amazonians often identify their languages as the speech of a particular place, such as "the speech of Pastaza River people." Within this river basin speakers may further break down their language as the speech of a more minor tributary. This tributary language is believed to be the speech not only of people but of the local plants and animals, who are thought to have spoken this language before acquiring their animal bodies. Hence, local plants and animals are included in the language of the place as audience, interlocutors, tropes, and metaphors (Swanson and Reddekop 2017). Ritual songs are sung to manioc plants, peccaries, or woolly monkeys. Humorous word plays imitate their sounds. Sound symbolic and evidential markers are used to evoke their presence in conversation. Bird songs, wind, and water carry love songs from wives to husbands over distances. Even where environments are similar, the distinct languages of neighboring tributaries engage the environment differently. As deforestation and local extinction of animals increases, the places become impoverished and the forms of speech that engaged them disappear. Similarly, when languages disappear so does a whole history of human cultural engagement with these places.

A clear example is the loss of species names. These names vary greatly from one river to another and carry a wealth of knowledge. For example, bird names are often onomatopoeic representations of the sound these species first uttered on being transformed from a previously human state. When the names are lost so is this reference to their origin stories and history. These names also carry with them systems of biological relation and classification (Berlin, 2014). In some languages, plants have animal names that evoke symbiotic relations or complex behavioral qualities used in healing. For example, one of the anthurium species is called 'trumpeter leaf' in Kichwa, because it resembles the tail of a trumpeter bird raised in its marching gait. Because the bird steps high as it marches, the leaf is applied as a poultice to cure the legs of children with difficulty walking. Through the poultice the bird behavior is transferred to the child, not only through the similarity in the leaf but also through the species name. When the plant species name is lost, so is the behavioral analogy to the bird as well as its use in medicine. Related to these losses is the distinctive Amazonian relation to nature embedded in native languages. For example, while native languages use the same terms to portray animal and human bodies, European languages embed ideas of human superiority to nature by using separate terms to distinguish the cultural quality of the human body (hands, fingernails) from those of animals (English: paws, claws; Spanish: patas, garras) (Nuckolls and Swanson 2020: 71). When a European language replaces a native language the distinctive relation to nature it carried is lost as well. So embedded are Amazonian languages in their micro-environments that the loss of species impoverishes language diversity and vice versa. Another area of loss are the place names of rivers and mountains, which carry with them a long history of local geographical knowledge.

With regard to the connection between Indigenous languages and knowledge of the medical uses of plants in the western Amazon, recent research by Cámara-Leret and Bascompte (2021) indicates that such knowledge tends to be linguistically specific. Compared to North America and New Guinea, the "linguistic uniqueness" of Indigenous medical plant use is highest in the Amazon region; 91% of knowledge of medical use of plants is limited to a single particular language. In other words, in 91% of the cases observed by Cámara-Leret and Bascompte, the medical use of a particular plant is not shared by speakers of different languages, but unique to one language, and therefore also highly culturally specific. The research has shown that this is independent of the level of endangerment of a particular plant or language, or to what clade or language family they respectively belong. However, this high degree of language specificity of Indigenous medicinal plant knowledge implies that when a language disappears, such knowledge is lost forever.

Another important area of loss is the language of social relations. Amazonian languages also helped maintain social order and cohesion through the use of kinship terms, evidential markers that recognize the speech of others, and grammatical elements that express emotional delicacy, politeness, and endearment. As the social environment came to include more complex relations to unrelated citizens of the state, this language of tenderness and refinement came to sound inappropriate, diminished, and disappeared. With the loss of such ways of expression, entire systems of conviviality that developed over centuries are lost (Gow 2000). Finally, contact with other languages may influence not only the vocabulary, but also the grammar and sound system of a language. Consequently, Indigenous languages may nowadays lose some of their most distinctive features through Spanish or Portuguese influence. For example, the Amazonian language Kichwa tends to favor verbs and adverbs more than nouns. Although Kichwa uses a small set of verb roots, this is amplified by an impressive range of sound symbolic ideophones and gestures that further qualify the events expressed by verbs (Nuckolls 1996). This gives the language a highly developed capacity for evocation, ambiguity, subtlety, multivalence, and nuanced use of perspective. At the same time, although it has impressive grammatical possibilities for the nominalization of verbs, it lacks the abstract nouns now common in technical, scientific, and business discourse; as well as the broad range of illocutionary verbs such as ‘threaten,’ ‘promise,’ ‘order,’ ‘conclude,’ which facilitate precise legal and technical communication in European languages (Nuckolls and Swanson 2018: 179). Through sustained contact with European language education, the native language of especially younger speakers may suffer the loss of certain specific phonological distinctions, such as tone and laryngealization, and grammatical distinctions, such as evidentials and perspectival markers. For example, the elaborate noun case system used by older Wao Tededo (isolate) speakers in Ecuador is rapidly disappearing in the speech of younger people. Younger people accustomed to writing are also much less likely to use the gestures and ideophones that characterized the story telling of their elders.

12.11 Importance of Indigenous languages in new contexts

Among the many drivers of language change there are also some that favor the flourishing of native languages. In recent years, the Amazon has seen a surge of connectivity through social media, particularly Facebook and WhatsApp. Many young members of even remote groups now have accounts. In fact, it may be that the more isolated the communities, the more avidly young people seek the connectivity that these media afford. While social media are certainly creating a flood of messages in national languages, they also provide a new forum for native languages. Whereas migration drives language loss by taking away a public domain where an Indigenous language can be dominant and free of discrimination, social media counter this trend by creating a new private spaces that may connect communities of speakers without fear of discrimination. Furthermore, because social media are informal and not used by older monolinguals, Indigenous language speakers text each other without having to worry about mixing in Spanish or Portuguese, or even switch to these languages in mid-sentence.

Another driver of language change countered by social media is the hegemony of national languages in broadcasting news, arts, entertainment, and sports. While cost and government licensing previously limited native access to the airwaves, native broadcasters are now flourishing on social media, avoiding these controls. Most Amazonian countries now have networks of native language communicators active on social media, even in smaller languages like Wao Tededo, Secoya, or Kofán in Ecuador. In some cases, these may be informal but also include more formal institutional voices such as the communication directors of the Indigenous Nations or organizations. A Shipibo migrant, for example, can now tune in to a variety of Facebook offerings featuring local sports news, church services, community meetings, ceremonies, and traditional music all streamed in Shipibo through the *Red de comunicadores indígenas del Perú, filial Ucayali* with names like *Shipibo Communications* and *Radio TV digital Shipibo*. Furthermore, pan-Indigenous activists in the western Amazon now typically have Facebook friends from Brazilian groups as far away as the Xingu. Hence, they are aware of native language pride and revitalization across the Amazon. To some degree social media are also countering the loss of older forms of language. Just as there are now citizen scientists recording biological species counts on cell phones, there are also young citizen documenters recording their grandparents' origin stories, songs, or other forms of ritual speech with cell phones and posting them to YouTube, Vimeo, or Facebook. Although inadequate for documentation and the creation of a lasting record, cell phone recording and posting may raise awareness of endangered forms of speech among other young activists who may follow the example. Finally, the internet opens up important new avenues for Indigenous language education in the territories, limiting migration. For example, smaller schools may use distance education. Native language YouTube videos recorded by elders in neighboring communities can be used in classes where the teacher may have limited knowledge of the local language.

Thus, although most drivers of change associated with modernity work to decrease language diversity, there is hope that others may counter these forces by providing new avenues for its preservation and revitalization.

12.12 Conclusions

This chapter presents some of the amazing diversity of Amazonian languages, their vitality, and their vulnerability to loss. Most of the Amazon's linguistic diversity is concentrated in the west, with fewer language families in the east. Coincidentally or not, this difference corresponds roughly to geological divisions, with the western Amazon covering younger Andean alluvial soils with greater biodiversity, and the eastern Amazon older, more weathered soils with less biodiversity. The striking correlations between biological and linguistic diversity are discussed in Chapter 10.

The linguistic diversity of the Amazon is highly endangered, perhaps even more so than biodiversity. The accelerated disappearance of languages can be attributed to five centuries of colonization by Europeans and their descendants, who brought disease, poverty, violence, and genocide to local populations. After the 1970s the effects of globalization were added.

Each language represents the heritage of centuries of cultural and intellectual creativity that holds scientific and cultural value for humanity as a whole. With the loss of each culture and each language, humanity loses yet another alternative and possibly unique way to understand the world around us. The survival of a language is interdependent with the integrity of its community of speakers, which again is often tied to the legal and ecological protection of their lands. With the loss of a language the sense of being a distinct people with the right to a territory is often weakened. It is hard to overestimate what is lost when an Amazonian language disappears.

To counter these losses, Indigenous peoples are calling on linguists to help them document and codify their languages by audiovisual registration, creating orthographies, and compiling dictionaries. Furthermore, Indigenous organizations throughout the region have pressured their governments to guarantee rights and formal recognition of their languages and to establish bilingual education programs. This has resulted in substantial progress in gaining legal status and bilingual education rights, especially for the larger languages. Sobering challenges remain, however. Often policies remain mostly on paper, with initiatives to protect the Indigenous languages greatly underfunded and understaffed.

12.13 Recommendations

In order to turn the tide on the disappearance of Amazonian language diversity, the factors that endanger its survival should be confronted. This section contains a number of recommendations that are directly or indirectly beneficial to language maintenance in the Amazon.

- Reliable national censuses on languages, including population and speaker numbers, proficiency levels, and sociolinguistic situation, carried out by professional linguists, can help governments know which languages exist and what is their situation. Such knowledge is essential for public policies and awareness campaigns.
- Indigenous communities should be consulted about their priorities with regard to language policies, and their demands should be met.
- Bi- or multilingualism should be valued rather than considered an obstacle, both by society at large and by Indigenous communities themselves. One does not have to abandon one's native language in order to learn a national language.
- Indigenous education should be improved and high-quality educational material in Indigenous languages should be developed.
- The professional study and documentation of Indigenous languages should be supported by governments, because the results of such work also form a necessary basis for the development of adequate educational materials and improve the chances for successful public policies with regard to languages.
- Indigenous territories must be protected against ecological degradation and the presence of outsiders should have the informed consent of their populations.
- Unsustainable development should be avoided and economic alternatives should be offered instead.
- Isolated Indigenous populations should not be contacted unless they themselves take the initiative.
- Indigenous languages, cultures, religions, and other aspects of Indigenous life should be respected by society in general. This requires adequate educational curricula, awareness campaigns, and replacing stereotypes and myths with reliable information. Only a public informed about diversity and its advantages is in a position to value, defend, and help preserve it.

12.14 Acknowledgments

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Amazon Assessment Report 2021

Chapter 13

African Presence in the Amazon: A Glance

Foto: Amazon Conservation Team

INDEX

Graphical Abstract

Figure 13.A From the 15th century, a significant exchange of biodiversity took place between Europe, Africa, the Caribbean, and the Americas. This is known as the Columbian Exchange. Paying attention to this type of interchange between tropical regions is central to conservation strategies. Exchanges between tropical regions of Africa and tropical regions of America were more extensive and complex in terms of genetic resources and knowledge than those between other regions with less biodiversity. Indeed, people, merchandise, culture, genetic material, and ideas traveled back and forth between slave ports on the western coast of Africa and many different tropical regions of the Americas: the Caribbean, the northern and western coasts of South America, and the eastern coast of South America. These routes were direct or indirect paths into the Amazon region.

This image focuses on one portion of the Columbian Exchange: Africa's contribution to the tropical regions of the Americas. African knowledge played a very important role in terms of the adaptation of African biodiversity in the Americas. In fact, one of the main purposes of Chapter 13 is to shine a light on the role Indigenous knowledge from tropical regions in Africa played in tropical regions of the Americas, as underlined by many prominent scholars. Therefore, the image portrays plant and animal species and human activities representing knowledge and beliefs of African Indigenous peoples traveling on slave ships to the tropical regions in the Americas.

The species in the image are a small example of the wide range of Africa's biodiversity brought on slave ships in order to survive the Atlantic crossing. Most of them became part of the New World's societies and everyday life. Upon their arrival, African domestic animal and plant species needed to adapt to the conditions and contexts of the New World. Both slaves and Maroons developed very biodiverse livelihood systems so that the aforementioned could adapt and survive to new conditions. The Graphical Abstract portrays contributions including knowledge of ecosystem management and biodiversity; food and medicinal plant species (H, I, L, M, N, O, P, Q, R and S); domestic animals (J); agricultural techniques and practices (A, B, E); belief systems and nature (D); Construction, handcrafts, and culinary practices (C, F, G and I), and of course, music. These are African peoples' assets for resilience in the Americas. Many of these assets are today part of Latin American culture. Resilience practices of African slaves and Maroon peoples were extensively nourished by Indigenous Peoples' knowledge from tropical regions in the Americas. Moreover, in agricultural systems on both continents, a mixture of agrobiodiversity from tropical regions in Africa and tropical regions in the Americas is found. The African legacy in the tropical regions of the Americas is as vast as it is bitter.

A. Agricultural knowledge; B. Pestle (heavy club-shaped object); C. Pottery and carving traditions; D. Sacred drums and musical instruments; E. Old African tools; F. House construction and roofing; G. Traditional weaving; H. Coffee nuts; I. Jollof rice; J. Goats, sheep and cattle; K. Kola nut; L. Hibiscus; M. Pearl millet (*Pennisetum glaucum*); N. Watermelon (*Citrullus lanatus*); O. African rice (*Oriza glaberrima*); P. Black-eyed pea; Q. Spices; R. okra (*Abelmoschus esculentus*).

African presence in the Amazon: A glance

Martha Cecilia Rosero-Peña[a]*

Key Messages

- African enslaved people arrived in the Americas from tropical regions where they had managed ecosystems and engaged in agriculture and the domestication of species for millennia. Slave ships not only transported enslaved African Indigenous people and genetic resources such as plants and livestock, but the people also brought with them critical knowledge about the adaptation of species for agriculture and livestock in the Americas. Many species found in the daily diets of American societies are of African origin. This knowledge has contributed to positive transformations of tropical landscapes in the Americas.
- A commonly overlooked element in the history of the Amazon concerns the presence and roles of peoples of African origin in the region. Research work on the contribution of the Afro-descendant population to the Americas has been more prolific in non-Spanish speaking countries.
- The history of the peoples of African origin in the Amazon offers contributions to research that can support conservation policies. It is central to support research vis-à-vis biodiversity, languages, ecosystem management, and techniques. Afro-descendant communities inhabiting the Amazon region are strategic actors in the conservation of tropical rainforests, biodiversity, ecosystems, watersheds, and sustainable agriculture.
- Livelihood systems of Afro-descendant peoples are highly biodiverse in terms of the species and ecosystems involved. Scientists consider the management carried out by Afro-descendants in various forested regions of tropical regions in the Americas, such as the Amazon, to be very positive in terms of landscape transformation.
- There are significant differences between the eastern and western regions of South America in terms of the general perception of the Afro-descendant presence in the Amazon. One reason could be the geographic location of the Amazon relative to the locations where Spain, Portugal, and Holland founded cities and built ports on the coasts of South America. In Brazil and Suriname, slave ships were disembarked in ports and cities that facilitated direct entry to the Amazon region. In the Spanish Empire, slave ships supplied enslaved Africans and merchandise to economic activities and populations placed in regions located from the Andes mountain range to the west. In the case of the western region of South America, reaching the Amazon requires crossing the Andes. Regions to the east of the Andes were considered wild areas not in control of the imperial authorities, in which Maroons and those who fled from the law took refuge.
- Colonial stereotypes still play a central role in the perception of the Afro-descendant population in South America, especially in the western Amazon. Stereotypes and racism are reflected in public policy, the exclusion of these groups from society, and their expulsion from the tropical forest they inhabit ancestrally.

Abstract

This chapter aims to advance understanding of the history of peoples of African origin in the Amazon and other tropical regions of the Americas. There is an emphasis on patterns of settlement and traditions of

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natural resource use and management during the two main periods in the history of African peoples in these regions: slavery and the post-abolition or freedom periods. It draws on two foundational approaches that illustrate contributions to genetic resource adaptation, knowledge, belief systems, and management practices that have generated positive tropical landscape transformations that include natural resource management practices up to now: the cultural exchange perspective and the socio-historical approach. The chapter centers on three countries: Brazil, Suriname, and Colombia. Geographic and sociological explanations for the invisibility of peoples of African descent in both academic research and policy in Latin America and the Amazon region are stressed. Additionally, this chapter suggests that there is a need for Amazonian scholars to have a better understanding of natural resource management by African descendant peoples. Finally, people of African descent should be considered one of the key actors for developing conservation strategies. It is essential to include them in scientific research and development policy approaches for the Amazonian region.

Keywords: Peoples of African origin, resource management, African botanical legacy, livestock, agrobiodiversity, traditional African religions, belief systems, Maroons, Cimarrones, Quilombola communities, Palenques, social and historical environmental perspective, resilience

13.1 Introduction

A commonly overlooked element in the history of the Amazon concerns the presence and roles of peoples of African origin in the region. Conventional histories rightly emphasize the roles of Indigenous peoples, European colonizers, and subsequent groups of migrants. African peoples also comprise part of that history, but their contributions have been routinely overlooked and thus undervalued. This is profoundly problematic because their patterns of land settlement and traditions of resource management have contributed in important ways to knowledge about sustainability in the Amazon and in other regions in the Americas. The story of the peoples of African origin in the Amazon offers contributions to research that can support conservation policies.

This chapter recounts the story of Afro-descendants enslaved in tropical regions in the Americas, particularly the Amazon. It adopts a social and environmental historical perspective as well as a cultural exchange approach. These perspectives make it possible to focus on how people of African origin contributed to sustainable management practices in different phases of adaptation to tropical landscapes. We review the history of these populations in the Amazon during two key phases: the slavery period, when they were either forced to work on plantations or escaped into forests and created Maroon societies; and the post-abolition or liberation period, when Afro-descendant people gained access to natural resources and exercised greater freedom and autonomy.

The chapter employs both socio-environmental historical and cultural exchange approaches to show how Afro-descendant populations have pursued sustainable resource management in regions of high biological diversity, such as the Amazon. Although other cultural groups, such as Indigenous peoples, have similarly contributed sustainable management practices, peoples of African origin have made a distinct contribution by drawing on traditions and religious beliefs from their ancestral territories (Cabrera 1954). Crucial to understanding the practices of African origin peoples in the Amazon and elsewhere in the American tropics have been multiple strands of thought in Afro-Latin American studies, in which the work carried out by Afro scholars and activists have been central. Such research work calls attention to the contributions of African origin peoples to sustainable resource management in the Amazon (Cabrera 1954; Brandon 1991; Arocha 1998; Carney and Acevedo Marín 2003; Garcia and Walsh 2017; Oliva 2017).

The chapter discusses the routes of the slave trade, linking origin sites with destination sites in tropical regions of the Americas. Highlighting ports of arrival is key to making sense of the migration of African origin groups to and within different countries that share the Amazon Basin. There is a particular focus on three countries in the Amazon Basin to which African slaves were taken: Brazil, Colombia, and Suriname. Slave ships forcibly embarked Africans, mainly along the culturally and ecologically diverse tropical coast of West Africa. Consequently, slave ships transported Africans of different ethnic groups with diverse systems of knowledge, culture, and spirituality. The Middle Passage across the Atlantic was a daunting test of survival for enslaved Africans (Carney and Rosomoff 2009). Those who survived brought deep knowledge and broad expertise in the management of tropical habitats. Similar to Indigenous societies of the Amazon, Africans often came from rainforest regions and had their own long-standing pools of knowledge, spiritual beliefs, and profound experiences that they then applied. Moreover, slave ships transported diverse African plant biota, which later became part of the economy and diets of New World societies, in a great measure owing to the know-how of people of African origin (Wood 1996; Carney and Rosomoff 2009; Van Andel 2010)

The second part of this chapter focuses on the knowledge and practices of enslaved people, especially on the natural resource management strategies of African-origin peoples, emphasizing how agroecological practices allowed them to adapt to new ecosystems and thereby sustain themselves. Agroecological strategies were applied both by enslaved African origin groups as well as by Maroon communities of slaves who escaped. In both situations, Afro-descendants used agricultural strategies in which they imitated forest vegetation strata with diversified crops and incorporated agrobiodiversity among specific crops, which permitted adaptation to new tropical environments, including the Amazon. As a result, Maroon settlements in various parts of the Americas are considered refuges for high biodiversity, owing to local knowledge, rituals, and practices (Carney and Voeks 2003; Legrás 2016; Carney 2020). Populations of African origin have made a significant contribution to sustainable resource management practices in the Amazon by drawing on traditional practices from tropical ecosystems in Africa and adapting them to tropical ecosystems in the Americas. Besides, traditional African religions, their social values, and rules have played a central role in natural resource management. Although peoples of African origin adapted their belief systems in the Americas, the intrinsic bond between individuals, society, and nature inherited from Africa continues as the foundation of the spiritual rules constructed in the diaspora (Eneji *et al.* 2012; Ekeopara and Ekpenyong 2016)

While African origin peoples made important contributions to knowledge about sustainable resource management practices in the Amazon during the colonial period, in the 19th century, and despite the liberation of slaves, white racism and societal segregation persisted. The result was that hegemonic white society ignored African origin contributions to sustainable management. In terms of African religion, beliefs were considered witchcraft, condemned, and ostracized by the Catholic Church. Furthermore, western science also ignored these contributions, as it was similarly dominated by whites. This helps explain the obscurity into which African origin contributions fell, an obscurity from which they are now being rescued, notably by Afro-Latin American scholars.

Afro-descendant communities have navigated this socio-political environment since the laws to abolish slavery were enacted. Humid tropical forests continued to be an alternative livelihood for Afro peoples in the post-slavery period (Leal 2004; Leal and Van Ausdal 2014; De-Torre 2018). Carney (2020) warns us about the return of the plantation era, which is evident today in countries such as Brazil and Colombia. Humid tropical forests that were once considered unhealthy and unproductive by dominant Latin American societies are today being destroyed by conventional agriculture. At the same time, western societies are forcibly displacing Afro and Indigenous peoples from their ancestral territories in many rainforest regions. In contrast, biodiverse ecosystems in the Amazon and elsewhere in the tropics of the Americas could be sustainably managed by recognizing the agroecological practices of peoples of African origin. The “Plantationocene” threatens biodiverse ecosystems such as those in the Amazon, as well as the cultures that could sustainably manage them (Carney 2020).

Throughout the text, this chapter highlights central messages that make evident several gaps of information and research on the African presence in the Amazon to inform effective policy design. Lechini (2008) asserts that ignoring Afro-descendants in scientific research on the social, cultural, and history of Ibero-American countries is an incomplete task. This chapter adds to this assertion the need to include the environment, agroecology, and management of tropical ecosystems in this equation. Therefore, research studies to inform conservation policy need an interdisciplinary perspective that identifies and takes the contributions of African populations into account. An interdisciplinary approach in research should consider the differentiated perspective as a path to understand and include the singularities of African descent in the Amazon region.

The need to support research vis-à-vis biodiversity, languages, ecosystem management, and techniques in contexts of Afro-descendant communities allow for better understanding of livelihood strategies and the associated relational ontological knowledge. Besides, it is essential to include Afro-Latin American scholarship in research and policy design, particularly that of Afro-Latin American scholars, to gain a broad understanding of the African descent social group and the current situation they face in the region. Furthermore, a better understanding of the contributions of Afro-descendants to tropical America requires promoting research on non-English-speaking countries of the basin where research on Afro-Amazonian peoples is very incipient. Efforts to consider African descent as key actors for the conservation of regions like the Amazon would be uncertain and sterile if they do not count and include the Afro-descendants themselves and their own research interests.

On the other hand, considering Afro-Amazonian groups as strategic actors for conservation, sustainable development, and governance is a challenging task in countries of the Amazon Basin. African descent communities have been invisible in Latin American society and government programs. A pernicious myth that Afro-descendant and even Indigenous groups are incapable of making decisions persists today. The above-mentioned differential approach is a pathway to address structural racism and inequality since it takes into account the cultural diversity of the Amazon.

13.2 The presence and roles of peoples of African descent in tropical regions of the Americas: An interdisciplinary crossroads

The ideas proposed in this chapter are located at the interdisciplinary crossroads between the sociological, historical, and environmental aspects related to the management of biodiversity and the livelihoods of Afro-descendant societies in the Amazon. Specifically, the chapter explores the contribution to agrobiodiversity and the management of tropical contexts by African Peoples who arrived in the Amazonian regions of Brazil, Colombia, and Suriname. Two frameworks enable this interdisciplinary approach; firstly, the cultural exchange perspective developed by major scholars whose research offers crucial clues to track the agrobiodiversity of enslaved Africans in the Americas. This perspective can also support the contribution of freed Afro-descendants to their continent of origin. Secondly, there is the socio-historical perspective in the post-slavery era, which helps us illustrate the ability of peoples of African origin to manage natural ecosystems and the changes they implemented in search of their livelihoods. These groups have struggled to sustain themselves culturally, socially, and economically without the resources from fair reparation after the abolition of slavery.

13.2.1 Slave traffic, ports of arrival, and entry into the Amazon

This section presents some regions of origin of enslaved Africans and the ports where slave ships were disembarked in South America. The chapter focuses on three countries to illustrate differences in African descent presence in the Amazon region: Colombia, Suriname, and Brazil. Colombia represents the western Amazonian countries, in which there is less perception of the African presence in the Amazon. Nevertheless, Colombia has Afro-descendant communities. In addition, the Colombian Constitution recognizes the collective character of the Afro territories and can facilitate local governance and self-determination. Brazil and Suriname are countries with significant African-descent populations in the Amazon. Slave ships were disembarked at the gates of the Amazon region, and many enslaved Africans managed to run away. Currently, there are multiple Maroon communities with organization processes inhabiting and managing various ecosystems in the tropical rainforest. Additionally, this chapter considers some central elements that mediate commercial dynamics on both sides of South America, which have played a role in the internal migration and the arrival of slaves to the Amazon region (Borucki 2009; O'Malley and Borucki 2017).

During the 400 years that the African slave trade lasted, more than 80,000 trips were made and approximately 12.5 million people were transported, mainly in the hands of Britain, France, Spain, Portugal, and the Netherlands (Eltis 2001 p. 42; Romero 2017). Europeans sourced their human merchandise along the west coast of Africa in the countries that are now known as Togo, Benin, Nigeria, Angola, Ghana, and Guinea. They named the west coast of Africa the "Slave Coast" (Figure 13.1). At the end of the 18th century, slave traffic increased to fifteen thousand African people per year (Miller 1989).

It is important to highlight the role of both the maritime slave market and the dense network of trafficking within South America, which included multiple routes, trans-shipments, and transactions between merchants. These commercial dynamics directly or indirectly affected the arrival of slaves in the Amazon region, especially in western South America. O'Malley and Borucki (2017) underscore the importance of the initial disembarkation of African captives in the New World to understand the internal slave trade within South America. An African person reaching his or her final destination can be considered a survivor of the transatlantic slave trade odyssey. During this journey, a person was sold and bought several times within the dense traffic network, which included different ports in the Caribbean islands and multiple slave traders and intermediaries such as the Dutch, English, French, and Danish. As the countless transactions were taking place, an enslaved person faced extremely drastic situations including hunger, malnutrition, diseases, injuries, beatings, and abuse of all kinds (Newson and Minchin 2007). In addition, depending on the landing ports and destinations within South America, enslaved people were forced to march for several days through the diverse geography, enduring extreme climates such as the cold of the Andes. The journey within South America depended on many variables such as geography, the ruling empire and its laws, demand for labor, and transportation costs. To meet the demand for slave labor in western South America, the voyage of an enslaved person could also include overland journeys down the Pacific Coast (Maya 1998; O'Malley and Borucki 2017).

13.2.2 Advancing within South America

Spanish and Portuguese domination of South America influenced both the empires' incursion into the Amazon and the arrival of people of African origin. According to Granero (1992), Spanish incursion towards the Amazon was not as decisive and direct as that of the Portuguese in Brazil, or the Dutch, French, and English in the Northern Amazon.

13.2.2.1 Colombia and Panama: Indirect arrival in the Amazon region

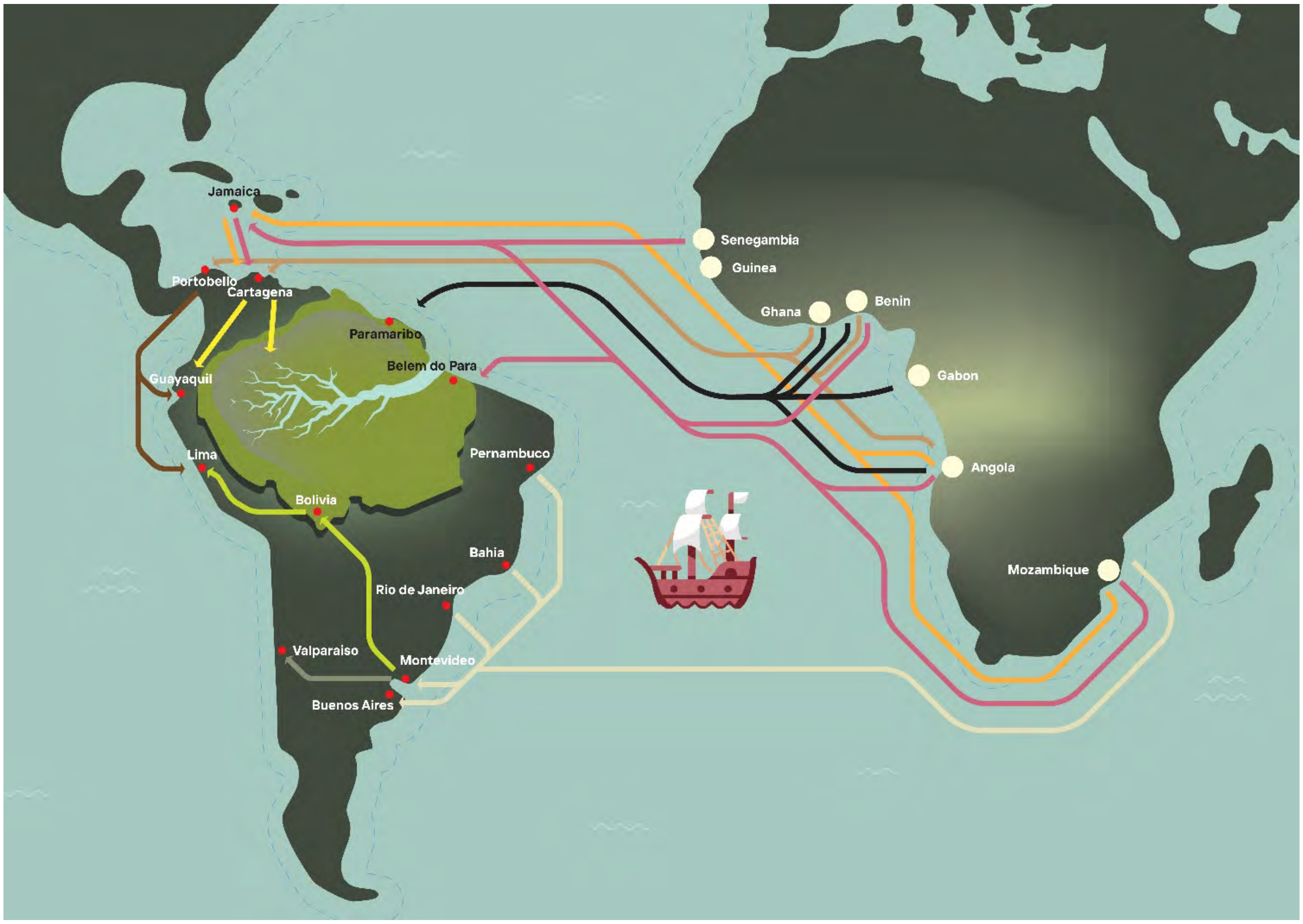


Figure 13.1 Slave Trade routes and main ports of disembarkment in South America.

In 1717, the Spanish crown founded the Viceroyalty of New Granada. This territorial entity facilitated both access to the western part of South America and also the navigation of two oceans, the Atlantic and Pacific. Furthermore, this geographical position gave Spain access to the Amazon via northwestern South America and the Andean Mountain range to the East.

On the other hand, there were several central routes for the transportation of enslaved Africans and merchandise to both western and eastern South America (see Figure 13.1). One route was from the ports of Cartagena de Indias in present-day Colombia, and Portobello in present-day Panama, to Guayaquil (Ecuador) and Lima (Perú) (Klein 1993; Maya 1998). The overland route from Cartagena to the southern regions used the navigability of large rivers such as the Magdalena and Atrato, along which merchants landed their human merchandise. Many captives were taken to the densely forested regions of northern Colombia (See box 13.1). Many enslaved people reached the region parallel to the Pacific Ocean. Others walked to the south throughout Colombia and arrived in Quito. Some other enslaved people had to walk along the Andes to Peru (Maya 1998; Romero 2017; O'Malley and Borucki 2017). In the middle of the 17th Century, Cartagena de Indias was already the main slave port in all of Hispanic America (Maya 1998 p. 7). The largest supply of slaves that entered through the Colombian port of Cartagena came from Benin, Angola, Ghana, and Guinea. The main ethnic groups were the Ararats, Lucumí, Zape, Angola, Congo, Viafara, Cambindo, Matambas, Carabalí, and Popó. Romero (2017) mentions that Africans kept the names of their ethnic groups and places of origin as surnames.

A route to transport African people to the southern Amazon and to other regions controlled by the Spanish used the South Atlantic Ocean merchant networks from Mozambique to Montevideo and Buenos Aires (Silva da Silva and Costa Barbosa 2020). Then, according to O'Malley and Borucki (2017), the Spanish made enslaved Africans march through the Rio de la Plata region to reach the Andean Mountain range in Upper Peru (today's Bolivia). Slaves often marched to Peruvian coastal markets and Valparaiso in Chile (O'Malley and Borucki 2017).

The journeys of enslaved people within South America have been very poorly recorded by historians. Furthermore, the arrival of enslaved people to the eastern Andes forest region and their participation in subsequent waves of migration to the Amazon has been minimally addressed in the literature. Renard-Casevitz *et al.* (1988) conducted an interethnic study on the first two centuries of Spanish colonization from the Ecuadorian Andes to the Bolivian Andes and the border with the eastern mountain jungles. The study reveals the presence of a population of African origin fulfilling various roles; colonial chronicles mention groups of Africans with the Spanish contingents loading cannons and opening roads. They also mention slaves searching for gold, working on sugar plantations, and participating in revolts with the Masiguenga Indigenous group from Peru. Scholars also underline the presence of settlements of Maroon blacks in the Amazonian foothills. During the early period of colonization, the border between the Andes and jungle regions such as the Amazon was not only ecological, but also epistemic; Castro-Gómez (2010) mentions the concept of an Andean region where civilization flourished in contrast to the natural and cultural savagery of the Amazon.

The mission to bring civilization and salvation that has been carried out since the early times of Spanish colonization was also carried out in Colombia. In Putumayo, blacks played a central role in the foundation of Mocoa. Despite the presence of African descent people and the evidence of *palenques* in the western Amazon of Colombia, study of the Afro population in this region is very new. Evidence of the presence of African descent people in the western Amazon Basin since colonial times merits anthropological, ecological, and sociological research lines similar to those that have been carried out in the eastern region of South America and the Caribbean, which allow comparative studies.

13.2.2.2 Brazil and Suriname: Direct arrival in the Amazon region

By the mid-1600s, the Dutch established their colony in the northeast of South America. Between the late 17th century and the beginning of the 18th Century, Curaçao was an important Atlantic center, from which shipments of slaves went to the Dutch colony of Suriname (O'Malley and Borucki 2017). An estimated 300,000 Africans arrived in Suriname as slaves, from regions between southern Gabon and northern Angola, Ghana, and Benin, mainly to work in sugar plantations.

The cruelty of Dutch masters caused many slaves to escape and take refuge in the dense Amazonian jungle. In fact, Thompson (2006) argues that sugar-producing countries had the most brutal labor histories and the most Maroon communities. Maroon communities in Suriname are different and have their own culture and language; these groups fought for freedom for about a century and managed to establish autonomous territories within dense tropical rainforests (Van Andel 2010). Suriname declared the abolition of slavery in 1863. Former slaves from coastal plantations mainly settled in the capital Paramaribo. At present, there are still 6 semi-independent Maroon communities with a total population of 72,553 (Vossen *et al.* 2014). Suriname is considered one of the places with the most significant ethnic and cultural diversity in the world, with 37% of the population from Asian Indian origin, 15% of Javanese origin, and 52% Afro-descendant (Moya 2012).

Box 13.1 Mompox Market

Mompox is the largest fluvial island in Colombia on the shores of the Magdalena River. Through the Magdalena River and the Cauca River, enslaved Africans entered the interior of the country. They were distributed towards the haciendas, the populated centers, and towards the Pacific region. The entire region through which these rivers run was covered by dense forests, which were a refuge for Maroons who eventually had commercial relations with urban centers. Let us remember that arrival to the Amazon through the western side of South America occurred indirectly in countries such as Colombia, Ecuador, and Peru, since their economies were established in relation to the Andes and the Pacific. Reaching the Amazon required crossing the high Andes mountain range.

Figure 13B.1 Marketplace, Mompox, Colombia, 1826. Entry routes to the western regions of South America and the Amazon ran from Cartagena de Indias and the main Colombian rivers. Source: Alcide Dessalines d'Orbigny, Voyage pittoresque dans les deux Amèriques (D’Orbigny 1853 p. 59) (Paris, 1836), p. 59, fig. 2. (Copy in Special Collections Department, University of Virginia Library) *Slavery Images: A Visual Record of the African Slave Trade and Slave Life in the Early African Diaspora*, accessed April 15, 2021, http://slaveryimages.org/s/slaveryimages/item/748 Rights: Image is in the public domain. Metadata is available under Creative Commons Attribution-NonCommercial 4.0 International.

Figure 13.2 The region established in the days of Columbus as "Terra Firma" is a zone of entry of commodities and enslaved people to South America and, therefore, to the Amazon region. The region consists of the modern-day countries of Brazil, Colombia, Ecuador, Guiana, Panama, and Venezuela. Map drawn by R. Bonne and others (1771). Source provided to Wikimedia Commons, the free media repository by Geographicus Rare Antique Maps as part of a cooperation project. https://www.geographicus.com/

On the other hand, slave routes to Brazil included ports in several regions of the West Coast of Africa such as Senegambia, West-Central Africa, and Bahía Santa Helena, the Gulf of Benin; and Southeast Africa, especially Mozambique (Arruda *et al.* 2014; Silva da Silva and Costa Barbosa 2020). The ports of Benguela and Luanda extended the Angola route, which was responsible for the straight offer of Africans as enslaved people to be sent to the Americas (Miller 1989, 1997; Ferreira 2012; Gardner *et al.* 2012). During the colonial period, slave ships arrived at the ports of Bahia and Pernambuco, far from the Amazon, because of the flourishing sugar economy.

Although extractive activities were considered of minor importance to the national economy, these were the basis of the Amazonian economy. Pará (Grão Pará) is a large state located in the Amazon Delta. The Portuguese used Belém do Pará to control access to the Amazon River (Legrás 2016; Silva da Silva and Costa Barbosa 2020). At the end of the 17th Century, Belém became the capital of the Amazon region. Slavery played a major role in the colonial Amazon region. African slaves were fundamental for the economic growth of the state of Grão-Pará and Maranhão. Upon disembarking, black slaves were transferred to the interior to labor in support of the Brazilian economy. Many slaves stayed in Belem to labor for the inhabitants, working as musicians, butchers, artisans, healers, and farmers (Alonso 2012; Silva and Saldivar 2018). In the mid-19th century, the boom in rubber extraction was the central economic activity of the Amazon region, as important to Brazil as coffee. This increased the requirement for slave labor. Sectors of civil society from Para, starting in 1869, promoted the need to emancipate all those who did servile work (Vergolino-Henry and Figueiredo 1990; Da-Fonseca 2011).

Research work on the contribution of the Afro-descendant population to the Americas has been more prolific in non-Spanish speaking countries. Therefore, it is essential to advance research on traditional practices from tropical ecosystems in Africa that were adapted to the tropical conditions of the Americas. On the other hand, we need to pay more attention to Afro-Latin American scholarship, notably that of Afro-Latin American scholars, to fully understand those practices in terms of their origins and adaptation.

13.3 The implications of being originally from tropical regions in the adaptation of enslaved Africans and their descendants in the Americas

Latin American societies, including certain academic tendencies, think African descendant groups owe their knowledge, culture, and actions to their contact with Indigenous Peoples from the Americas, Creoles, and Europeans. However, this outlook overlooks or ignores several aspects that have played a central role both in the resilience of African Indigenous peoples and their contributions to the economy and well-being of American societies.

When the Portuguese arrived to explore West Africa in 1443, Indigenous peoples had been building cultural and agricultural complexes for millennia; they had already domesticated many species that the world knows today and developed livelihoods and extractive systems in Africa's diverse tropical ecosystems (Foreign Office 1920; UNESCO 1959; Carney and Rosomoff 2009; Van Andel *et al.* 2014). Coming from a tropical zone was a significant advantage for Africans, when compared to Europeans and their ability to adapt to the American tropics. This can be observed in the agricultural systems and livelihood strategies of the peoples of African descent, both those enslaved and the thousands who fled to the jungle (*cimarrones),* as we will illustrate with examples from both the eastern and western parts of Latin America (Carney 2020). The floristic composition of African tropical forests and tropical regions in the Americas is very dissimilar; Vossen *et al.* (2014) assert that Africa and the Americas share only 1% of the total number of species, including weeds. African Indigenous peoples managed to survive by identifying similarities with the flora of their continent of origin and even renaming many species (Van Andel *et al.* 2014).

Furthermore, Latin American nations also overlook the fact that many of the economic activities that we know today in tropical regions of the Americas are alien to this continent. Some examples familiar to Latin Americans are livestock farming and agricultural activities that have expanded at the expense of tropical forests, transforming landscapes. Livestock farming originally come from Europe, Africa, and Asia; that is, the species of bovines, sheep, goats, pigs, grasses, and many other forage plants were imported to the Americas during conquest and colonial times (De-Mortillet 1879; Epstein 1971; MacHugh and Bradley 2001; Carney and Rosomoff 2009). Regarding agriculture, we can also say that many species and cultivation techniques are foreign to the Americas. Coffee and sugar cane became central in the global economy. These crops were cultivated at the expense of forests and enslaved humans. Furthermore, knowledge of African management of tropical ecosystems for livelihood would have been required to adapt plant and animal species to the conditions of South America. Evidence of the knowledge and contribution of Africans to the Americas regarding

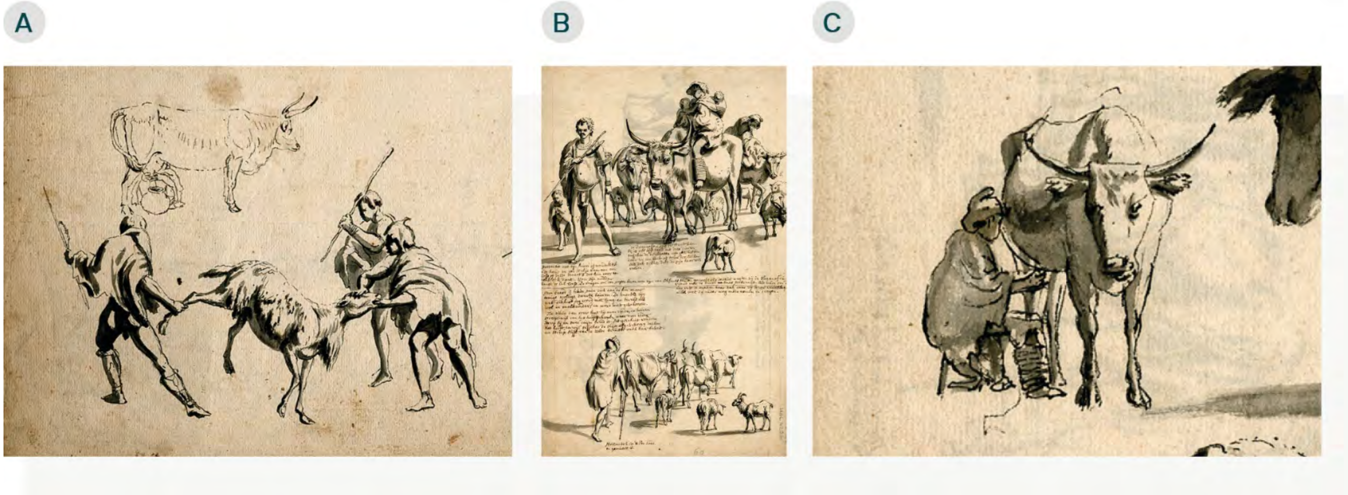


Figure 13.3 When the transatlantic slave trade began, ships transported enslaved Indigenous Africans and their knowledge about the cultivation of tropical plant species and the rearing of domestic animals unknown in the Americas at that time. The earliest realistic depictions of cattle from Khoikhoi (Western Cape, South Africa) were probably drawn circa 1713 or earlier. The cattle pertained to the Sanga breeds, which resulted from the interbreeding of the indigenous wild cattle found in North Africa and the Sahara 8,000 years ago with the humped Zebu introduced to Africa from Asia more than 2,000 years ago or earlier. A) Khoi man dealing with a recalcitrant sheep; B) Khoi family traveling with their domestic animals: oxen, sheep, goats, and dogs; C) Khoi person milking. Source: World Digital Library. The Library of Congress. With the support of the United Nations Education Scientific and Cultural Organization https://www.wdl.org/en/item/11278/. Download date: 02.04.2021

agricultural and livestock technologies has been studied by major scholars. These researchers have refuted the widespread belief that many agricultural techniques of tropical species were owing to European ingenuity. This is the case of rice (*Oryza glaberrima*), an emblematic African plant species. Rice cultivation became crucial in the Americas, which was adapted thanks to African knowledge (Wood 1996; Carney 1996; Carney and Rosomoff 2009).

13.4 Tracing African legacy in the Americas

Carney (2009, p. 5) mentions that the link between culture and the environment has traditionally been agriculture. Indeed, the African legacy in the Americas can be traced to both agro-biodiversity and knowledge of agricultural techniques, seed management, and adaptation to new environments as well as to culinary practices (Carney and Rosomoff 2009; Zabala-Gómez 2017).

This section discusses several interesting research approaches that emphasize the other roles of African populations, especially for conservation strategies and sustainable management of regions of high importance for biological conservation such as the Amazon.

Independent domestication of plant and animal species began between 13,000 to 15,000 years ago. Food production independently arose in at least nine areas of the world, and species and knowledge have traveled between continents at different times in human history (Diamond 2002; Gupta 2004). In Africa, the domestication of species could have taken two or three millennia to be realized (Carney and Rosomoff 2009). There are two important eras in which a significant botanical interchange took place. The Monsoon Exchange among regions of the Old World occurred between 300 BC and AD 700, and one of the routes — the Western Indian Ocean through Africa — contributed to the exchange of nearly 2,000 species of cereals, vegetable tubers, and legumes to Asia, thus helping to transform diverse food systems (Carney and Rosomoff 2009 p. 7; Seland 2014) The second era was in the 15th century with the Iberian expansion, which resulted in the so-called Columbian Exchange (Carney and Rosomoff 2009 p. 7; Van Andel 2010; Van Andel et al. 2014). Africans have plausibly contributed to global food systems, especially to those of the Americas. The exchange of plants of African origin to the Americas and the role of enslaved Africans in the adaptation of these species is also reflected in cash crops at plantations in the New World (Carney 2009, 2020). Species of southern Asian origin, such as plantains and bananas, arrived in Africa through the ancient food trade in commodities within the Old World, and they became crucial dietary staples long before the Portuguese began to explore the West African coast. Later, plantains and bananas became fundamental food staples in some tropical regions in the Americas from the so-called "Columbian exchange". According to Crosby (2003), during this time, there were crucial exchanges between the Old and the New World in terms of food crops, knowledge, and even diseases, which have been neglected by economics studies.

13.4.1 Slave ships and the cultural exchange between tropical regions of Africa and the Americas

The exchange of plants of African origin and the role of enslaved Africans in the adaptation of these species in the New World began precisely with the slave ships. Slave trade ships transported more than 12.5 million human beings, not including the ships' crew, and dietary staples that were crucial for successfully crossing the Atlantic were transported with the enslaved people. According to Carney and Rosomoff (2009), the ships were provisioned in different places on the West Coast of Africa, which supplied a wide diversity of plant and animal species for human subsistence. The *Oryza glaberrima* was introduced to the Americas as a food staple in slave ships; this species is cultivated today in America by people of African origin (Carney and Acevedo Marín 2003; Carney 2009; Carney and Rosomoff 2009; Van Andel 2010). Four thousand years ago, Africans domesticated rice along the so-called Rice Coast, which is the tropical area between Senegambia, Sierra Leone, and Liberia (Johnny *et al.* 1981; Van Andel *et al.* 2014). African species were displaced by Asian ones (*O. sativa* L.) when mechanical mills were introduced in the Americas. In the oral tradition of both the countries sharing the Amazon region and the United States, there is an account that African women smuggled rice grains in their hair, which allowed them to grow it in the Americas (Carney 2004; Van Andel 2010). In Colombia's Pacific region, traditional Afro-descendant communities have cultivated and milled rice in the tropical rainforest. According to key informants from the Noanamá, Chocó department in the aforementioned region (B. Murillo, personal communication, June 22, 2021), a very common practice used by elderly women forest dwellers when navigating rivers to visit urban centers was to hide valuable items such as money or gold in their hair. Several academics have highlighted the role of women of African origin in the agency, resistance, and resilience of the group (Carney 2009; Hurtado *et al.* 2018).

The cultivation of African rice was central to the economy of several countries in the Americas. Carney (2004, p. 13) comments that in 1775 in Brazil the cultivation of cotton and rice was promoted in the Amazon region — Belem do Pará and Maranhão — and African people were bought on the west coast because of their knowledge of the cultivation technique. Rice was also cultivated in sugar plantations, which had large numbers of enslaved Africans, such as in the Pernambuco region. In Suriname, anthropological studies recorded 74 rice names in the languages of the Maroon communities (Van Andel 2010). As mentioned earlier, the cultivation of African rice species (*Oryza glaberrima*) has been central in rice plantations and in the economy of the United States and South America. The cultivation and its technology have been attributed to the ingenuity of the plantation owners. However, the tracks of historical, archaeological, and ethnobotanical research carried out by major scholars on different contexts of the Americas present important evidence of the African contribution in terms of technology and agriculture for commercial and food crops of African origin. Coffee, okra, sesame, and kola nut, among other Afri-

Figure 13.4 A Fugitive Negro. Pierre Jacques Benoit (1782-1854) was a Belgian artist who visited the Dutch colony of Suriname in 1831 (Benoit 1839). The tropical ecosystems of the Americas were familiar places for Maroon people, taking into account that their places of origin were mainly tropical regions of Africa. "This engraving shows an escaped slave sitting in his shelter, with various utensils and goods, including rifle and canoe, by a river in the jungle." The author once encountered one of these fugitives in an almost impenetrable forest where he had lived for three years. "He had no family or companionship and lived off of crabs, monkeys, snakes, bananas, everything that nature offered. He had only ventured twice to Paramaribo, to trade various forest products for lead shot, powder, and gin". Rights: Image is in the public domain. Metadata is available under Creative Commons Attribution-NonCommercial 4.0 International.

can species, are also currently part of the food, agricultural, and gastronomic culture in particular of tropical America and the Caribbean (Clarence-Smith and Topik 2003; Carney 2009; Carney and Rosomoff 2009; Van Andel 2010; Harris *et al.* 2014; Van Andel *et al.* 2014; Agha 2016).

Another iconic native species from the tropical rainforest of Africa is the cola nut tree, the main ingredient in Coca-Cola. This nut is found in the cultivation systems of some Indigenous Peoples in the Amazon, which suggests that there have been cultivation shifts between the continents. Another exchange example is cocoa, which is central in the rural economy of Ghana.

13.5 Agroecosystems of Maroon and plantation slaves. Resilience strategies in tropical regions in the Americas

The Maroon phenomenon is reported both in the north and northeast region of South America, in the Caribbean (Thompson 2006), and in the western region of South America (De Friedemann and Arocha 1986; Renard-Casevitz *et al.* 1988; De Friedemann 1993; Maya 1998). Likewise, food staples from slave ships became the basic seeds for subsistence agriculture of escaped Maroons in the Americas. The survival of enslaved people who managed to escape depended on their skills and knowledge to obtain food supplies from new environments. Similarly, those communities depended on their Western and Central African knowledge and techniques in Maroon autonomous territorial spaces built in the middle of the jungles of tropical America (Maya 1998; Thompson 2006). In Colombia, some Maroon enclaves were dedicated to grazing Cebu cattle, cultivating peanuts linked to funeral rites, pig farming, and the fortified construction of *palenques*. These characteristics account for the tribes and places of origin of the African Indigenous peoples that arrived in Colombia via the port city of Cartagena de Indias.

Both plantation slaves and escaped Maroons depended on their medicinal, healing and magical, religious, and nutritional botanical knowledge, among others skills, to survive (Carney and Marín, 2003; Andel, Behari-Ramdas, Havinga, and Groenendijk, 2007; van't Klooster, Andel, and Reis, 2016). Andel et al. (2014) mention that African botanical heritage in the Americas is reflected in the subsistence practices of the groups that still inhabit tropical forests. Multi-cropping systems of many communities from the African tropical belt transformed the rainforest into a food forest, incorporating Amerindian staples such as corn, cocoa, sweet potatoes, cassava, and peanuts (Carney and Rossmoff, 2009; Carney and Acevedo, 2003 pp. 25, 88).

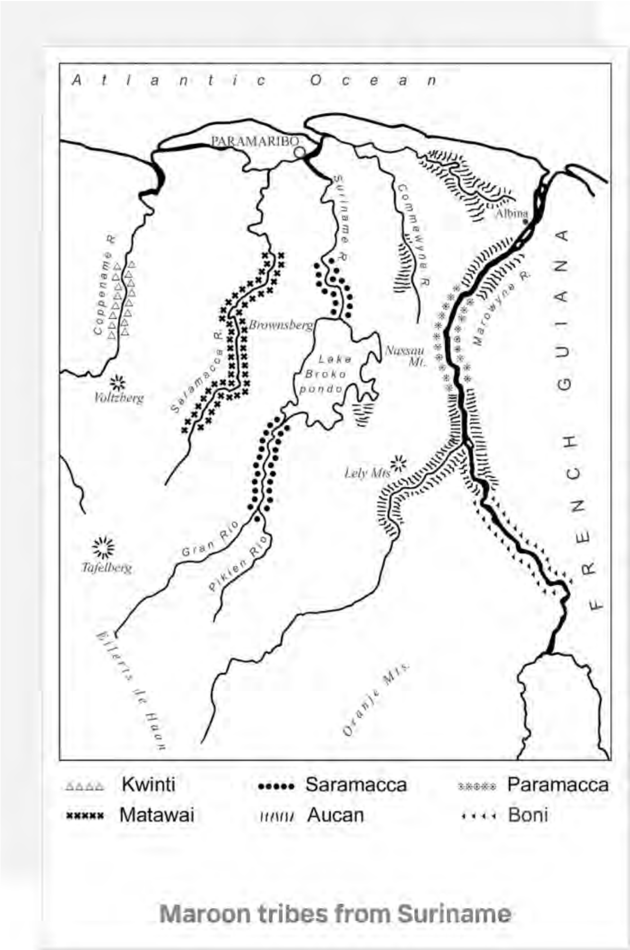


Figure 13.5 Maroon Tribes from Suriname. Illustration by H. Rypkema. Naturalis Biodiversity Center. Many African plant species that arrived inadvertently on slave ships helped Maroon and slave groups survive. However, new flora and fauna compositions forced these communities to construct their own classifications and adapt to a new environment. Source: Illustration by H. Rypkema. In: Van Andel et al (2014).

The word Kilombo comes from the warrior society of the Ovimbundil, a Bantu ethnic group from the plateau of central Angola whose language is mainly Umbundu and were in permanent conflict with Europeans. In Brazil, the Portuguese Overseas Council officially defined the settlement of fugitive enslaved Africans as *quilombo*. At the end of the 16th century, there were more than fifty sugar mills in Brazil and some fifteen thousand African slaves worked in them. Social scientists, archaeologists, and historians have studied the Maroon phenomenon in Palmares, Alagoas State, which is considered one of the most important in Brazil. These slaves came directly from the Bantu areas of

Figure 13.6 A) "View of the central vegetable, fruit and poultry market of Paramaribo in 1831 (Suriname) located between Dutch-style houses" (translation). The central role of African descendants in the food market is noted. Women played a central role in commercializing food in the eastern and northeastern regions of South America. These women were called 'higglers' in British colonies and *quitandeiras* in Brazil (Carney 2020; Carney & Rosomoff 2009). Goats are also observed, a foreign species to the Americas, as are cattle, pigs, and sheep. Vue de gran Marché aux légumes, fruits et volailles in Slavery Images, available: http://slavery-images.org/s/slaveryimages/item/2355 B) Milkmaid and black women carrying milk in Suriname. Source: "Figure 66" in Pierre Jacques Benoit, Voyage à Surinam; description des possessions néerlandaises dans la Guyane (Bruxelles: Société des Beaux-Arts de Wasme et Laurent, 1839). Rights: Image is in the public domain. Metadata is available under Creative Commons Attribution-Non-Commercial 4.0 International.

Angola and Congo in the 17th century. They established both local relationships with Indigenous peoples and with local and European merchants (Domínguez and Funari 2008; Stenou 2004). These settlements also housed Indigenous people, mulattoes, *caboclos*, escaped soldiers, and other individuals discriminated against by the majority of society. The same characteristics have been reported for other regions where there were settlements of fugitive slaves. Maroon communities are a repository of African plant resources, knowledge, and agricultural practices that slightly alter the natural forest landscape. Both food and medicinal species found in Maroon agroecosystems come from various tropical regions of Africa; Carney and Acevedo (2003) mention the western savannas between the Ivory Coast and Lake Chad, the central-western rainforest comprising Nigeria and Congo, and the eastern savannas between Sudan, Ethiopia, and Uganda. In addition to food species, enslaved Africans also brought medicinal plants. Carney and Acevedo (2003) argue that the Caribbean has a rich pharmacopeia, and of 82 identified medicinal plants, 43 are native to Africa.

13.6. Religion and nature

Populations of African origin have made a significant contribution to sustainable resource management practices in the Amazon by taking advantage of the traditional practices of the tropical ecosystems of Africa and adapting them to the tropical ecosystems of the Americas. African rice is considered a gift from God, and, like the rest of nature, is part of the worldview and traditional religion. Traditional practices have been evident in the adaptation of agricultural systems and plant and animal species of African origin in the Americas. Likewise, traditional African religions were transformed and recreated in the Americas, maintaining the intrinsic link between individuals, society, and nature described in the eschatological belief systems, principles, and codes of conduct of African societies (Ekeopara and Ekpenyong 2016; Eneji et al.

2012). Building from Escobar (2018), it can be said that Africans arrived in environments that facilitated the ontological relationship, allowing them to adapt and continue being in the world. The universal mother for the peoples of African origin is equivalent to the bush. According to the first lines of the most renowned book by Cuban writer and researcher Lidia Cabrera, "The bush is the place where everything arises from and the place where everything returns to. Everything is in the bush, the supernatural forces, the ancestors, the Orishas, good spirits and evil spirits ... life came from the bush, we [the Afro-descendants] are children of the bush" (Cabrera 1954). The groups of African origin developed different religions and beliefs such as the candomble in Brazil; Santeria, Ifa, and Abakua in Cuba; voodoo in Haiti; the orisha in Trinidad and Tobago; winti among the Creoles from Suriname; and various other beliefs among the Maroon. Something in common among new Afro-descendant religions is the central role that nature plays and the relationship that is established between the latter and human beings. A story that connects three continents through the transatlantic journey is that of the trickster-spider Ananse (Deandrea 2004). This is a mythical character from the Akan culture of southern Ghana and the Ivory Coast and is well-known among African Americans and Afro-Caribbean people. The character has also woven a net through South America. The trickster Ananse is central in art and literature in Brazil and Suriname. Ananse would have arrived at the Colombian Amazon through the Pacific Coast. The spider intrinsically connects Afro human beings with the ancestral territory and nature from birth rituals (Arocha 1999; Escobar 2018; Lozano 2017).

13.7 Agrobiodiversity, the resilience strategy in both slavery and freedom

Landowners and chroniclers of the Indies reported a great diversity of species in the food plots of slaves, among which was a great variety of species from both Africa and the Americas. Carney and

Figure 13.7 Images of Negroes' houses. Pierre Jacques Benoit (1782-1854). Agrobiodiversity in the dooryard and surrounding areas of the house. Multiestrata and Mixed-crop farming systems of Maroon and enslaved people for food, commercialization, medicine, and rituals.

Rosomoff (2009, p. 135) mention that these plots were called the botanical gardens of the Atlantic World's dispossessed. Plots became spaces for the adaptation of African seeds, many of which are still marketed both for human consumption and for industrial processes. Similarly, these authors mention the agrobiodiversity in the plots of plantation slaves reported in countries such as French Guiana, Suriname, the United States (the Carolinas and Virginia), Colombia, Cuba, Curacao, Jamaica, and Brazil, among others. Some of the species of African origin reported are cereals, including millet (*Pennisetum glaucum*), sorghum (*Sorghum bicolor*), and rice (*Oryza glaberrima*); tubers such as yam (*Discorea Cayenensis)*; musa, including plantain and banana (*Musa spp*.); taro/eddo (*Colocasia esculenta*); legumes, including black-eyed pea or cowpea (*Vigna unguiculata*), and pigeon pea or Congo pea (*Cajanus cajan*); beverages, including coffee (*Coffea spp*.), tamarind (*Tamarindus indica*), kola nut (*Cola spp,K*), and hibiscus/roselle (*Hibiscus sabdariffa*); oil plants, including sesame (*Sesamum radiatum*), castor bean (*Ricinus communis*), and oil palm/dendê (*Elaeis guineensis*); vegetables, including okra (*Abelmoschus esculentus)*, amaranth (*Amaranthus spp*)., and Guinea pepper (*Xylopia aethiopica*)*;* and fodder, including Guinea grass (*Panicum maximum*), Pará/Angola grass (*Panicum muticum*), and Bermuda grass (*Cynodon dactylon*).

Africans not only domesticated plants but have traditionally been pastoralists (Diamond, 2002). The tropical American lowlands did not have large domesticated animals. African cattle may well have made genetic contributions to the breeds that have proven to be suitable for the climatic conditions of the Venezuelan and Colombian plains and other regions of tropical America, such as the Argentine pampas. Likewise, grasses were scarce in the tropics, and many pasture forage species originated in Africa. This has been called "the Africanization of the New World's Tropical Grasslands" (Carney and Rosomoff 2009, p. 166).

On the role of agriculture in connecting culture and the environment, it is also possible to emphasize culinary practices as a cultural value in traditional societies, such as the Indigenous peoples of the Americas and Africa, which in turn integrates ecosystems and knowledge about their cycles and dynamics that very often include ontological foundations of these groups.

13.8 African roles in caregiving and production: African culinary and livelihood practices in tropical regions in the Americas

Both in the western and eastern regions of South America, the literature mentions the central role of enslaved African women linked to the preparation of food and to various domestic activities, both in plantations and cities (Zabala-Gómez 2017; Silva da Silva and Costa Barbosa 2020).

Cooking is a practice that attests to the African presence in the Americas. The ingredients of the foodways of Africa are still present in culinary practices of the diaspora. The ingredients and, very often, the names of recipes, are still of African origin and can be traced to various countries in tropical areas or regions of the Americas. The fufu of Ghana, Nigeria, and Cameroon is a stew of yam, mashed banana, and other starchy tubers to which meat is added (in the Dominican Republic it is called *mangú*; in Puerto Rico they call it *Mofongo*; in Cuba it is *plantain fufu*). In Colombia, a variant of fufu made with cassava and pigeon peas (*Guandul*) has been reported (Gómez 2017; Zabala-Gómez 2017). In the south western region of Colombia, rice (*Oryza glaberrima*) was not a food consumed by the elites during colonial times, but it was one of the agricultural products found in the vegetable garden plots of the enslaved. With the passage of time, rice became the fundamental base of the culinary tradition in the region (Gómez 2017; Zabala-Gómez 2017). Enslavedor Maroon women adapted rice dishes with greens and beans of African origin to the conditions of the regions of The Americas. The *arroz de cuxá*, for instance, is prepared with sorrel leaves (hibiscus). The name Cuxá comes from the Mandinka name for hibiscus (the kucha).

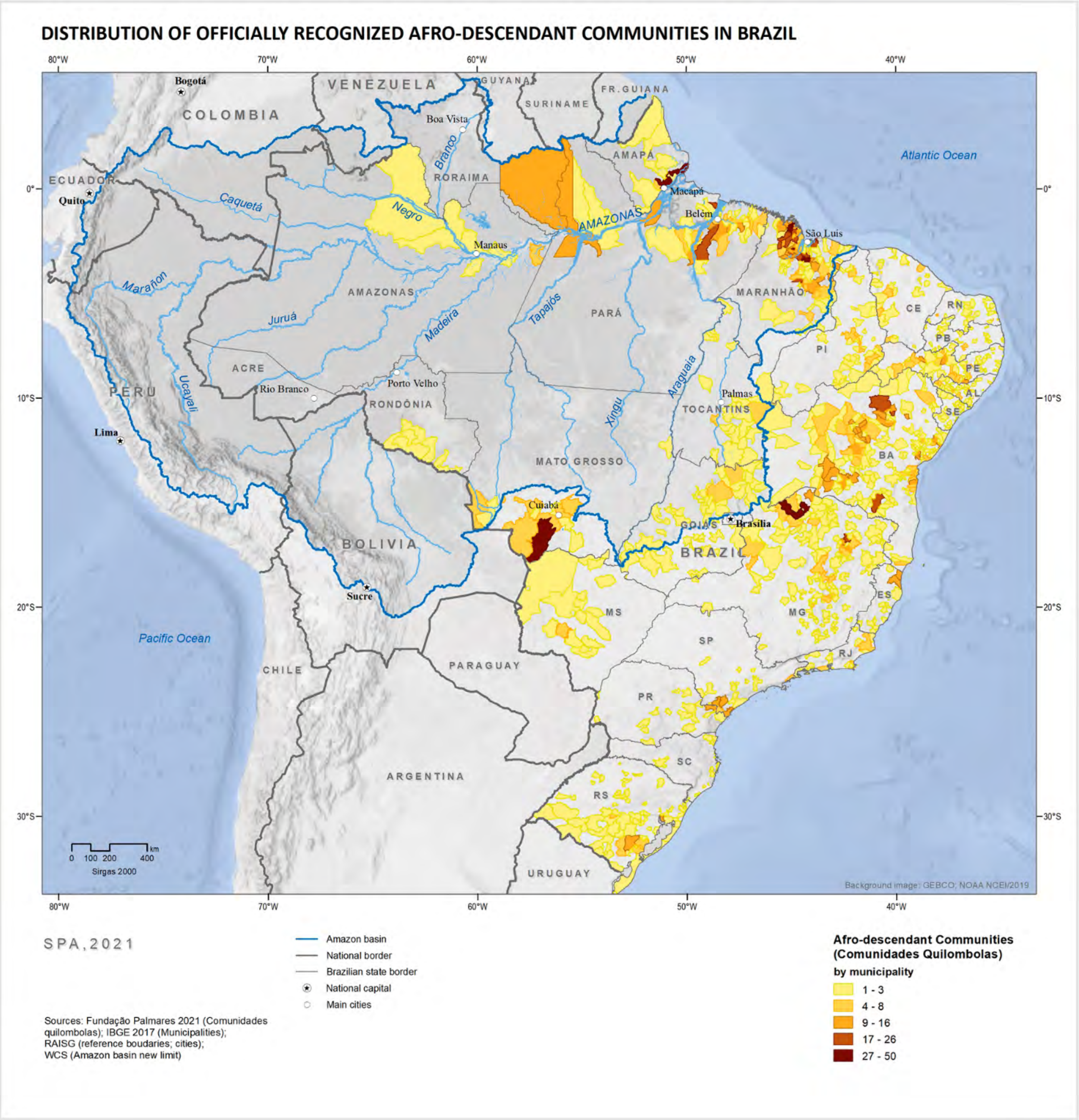
As suggested by Zabala-Gómez (2017), kitchens were spaces of freedom for enslaved people. The

Figure 13.8. Biodiversity and culinary practices in an Afro-descendant community forest territory in the Colombian Pacific region. Afro-Pacific groups migrated to the Colombian Amazon at different times seeking livelihood alternatives and freedom. A) an inventory of plant species associated with Afro-representative dishes, and their spatial distribution in an Afro family food plot; B) 21 different dishes and utensils that are woven or made in the Bubuey community of the Negros en Acción Community Council. Photo credits: Martha Rosero-Peña. Convenio SENA-Tropenbos, Colombia.

kitchen has traditionally been a social, cultural, symbolic, physical, and geographical space that, unlike others, was a place where enslaved people were not persecuted by slave owners. Kitchens could well have played an important role in the conservation of biodiversity linked to recipes, knowledge, and beliefs. The kitchen is linked to agriculture, family nutrition, and the health practices of Afro-descendants, who obtained species from different places in the forest territory to carry out many types of livelihood activities.

13.9 The Afro-Latin American contribution to Africa: A two-way cultural exchange

This document has mentioned several aspects of the Afro-descendant presence in the Amazon, in only one way: from Africa to the Americas. Could it be possible that the enslaved had returned to Africa at some point in history? In fact, after the abolition of slavery, the Brazilian diaspora in Africa started to form. Ferreira (2012), Law (1997), and Mann (1999) assert that during the centuries of slave trade, merchandise, culture, genetic material, and ideas traveled back and forth in the ships between the Slave Coast and Brazil. Microstudies, which include biographies and ethnographies, can account for aspects that macro- and global studies overlook, but which explain many shortcuts in history, such as why species from tropical regions of America are also cultivated and used in African contexts. There really was a cultural exchange that included hundreds of freed slaves who returned to West Africa from Brazil in the 1830s. They established continuing commercial, cultural, and intellectual communication with relatives and acquaintances who stayed in Brazil. It has been reported that some of those who returned sent money back to Brazil to purchase their children's freedom. This exchange may have been due to the fact that some ports in the Americas, such as Salvador de Bahia, had close contact with a certain region of Africa (Klein 1993). In both cases, the exchange included plant and animal genetic material, cultural and religious aspects, and knowledge about the cultivation techniques of the material exchanged between both sides of the Atlantic (Carney and Rosomoff 2009; Falola and Akínyẹmí 2017).



Sources: Fundação Palmares 2021 (Comunidades quilombolas); IBGE 2017 (Municipalities); RAISG (reference boudaries; cities); WCS (Amazon basin new limit)

Figure 13.9 Legally constituted territories of Afro-descendant communities in Brazil. The presence of descendants of African enslaved people is significant not only in the Amazon but in the vast majority of Brazilian territory. The country's geography facilitated the direct disembarkment of slave ships into the Amazon region. Counting on these communities for natural resource conservation strategies is very important due to the characteristics of their livelihood and nature management systems. Sources: Fundação Palmares Cultural (2021) WCS-Venticinque et al. (2016), IBGE (2017), RAISG (2020).

13.10 Research, history, and landscape transformation in freedom: A view for Afro-Amazonian contexts

Global colonization and decolonization policies have influenced academic interest in African descent in Latin America and the Amazon. Historical literature has frequently mentioned Afro-descendants since the Iberian conquest and the colonial periods. It is always possible to trace African origin people in history thanks to chroniclers, Catholic priests, historians, and slave traders. However, as soon as Latin American countries abolished slavery, African descent people disappeared from historical literature (Andrews 1994). Colonial deterministic doctrines and nineteenth-century social Darwinian thought influenced the Latin American political environment. Latin American countries pretended to portray a self-image of strength and racial superiority in the face of a world that was opening up to imperialism (Lechini 2008; Marquardt 2011). At the beginning of the 20th century, the whitening of social groups through miscegenation gained momentum in the development policies of Latin American countries. In 1922, in Colombia, the conjunction between ultra-conservative political interests and pseudoscientific studies influenced the perception of Indigenous peoples and Afro-descendants as obstacles for Colombian development. Miscegenation policy was also enacted to promote immigration of Europeans to whiten Colombian society (Castro-Gómez 2009).

Research focused on miscegenation between whites and Indigenous people obscured the Afro presence in Latin American society. In the mid-twentieth century, Afro-Latin American scholars raised the visibility of the neglected Afro theme in literature and in anthropological research. This coincides with African decolonization and an interest in systematic studies of the problems of the African descent population in Latin America (Lechini 2008). Afro-Latin American racial movements in Brazil and Colombia were motivated by political thought and the Afro-American civil rights movement. In response, both countries constructed more plural and inclusive national constitutions. Afro-Latin American movements started national debates on racial inequality after the national constitutions of Brazil (1988) and Colombia (1991). The Colombian constitution opens a door for both Afro-Colombian communities and Indigenous peoples to govern their territories with relative autonomy.

13.10.1 Brazilian *Quilombos* and Community Councils of the Colombian Pacific region: Reflections on invisible Afro-descendant groups in the Amazon

There is significant potential for biocultural conservation efforts in the territories of Afro-descendant peoples in Brazil, Suriname, and Colombia, taking into account their contexts and realities. Currently, Afro-descendant communities in countries such as Brazil and Colombia have made significant progress in titling lands they ancestrally inhabited. This path has been arduous as the abolition process did not consider compensation or land distribution. The Afro population throughout South America faced many difficulties and economic shortages in the post-abolition period. Afro communities in different regions of Brazil and Colombia have formed in different ways; there are still *quilombos* that formed in the colonial period, lands collectively purchased by Afro-free communities, communities on lands donated by neighboring slave owners to keep cheap labor close, and land donated by churches, among others. In the territories inhabited by Afro communities, they carry out livelihood strategies that allow biodiversity and the use of different types of ecosystems, maintaining a rural/urban relationship linked to local and national markets (Leal 2004). This is a livelihood approach that has allowed them to survive since their arrival as slaves in the forested regions of several countries in the basin.

13.10.1.1 Brazil

The Institute for Colonization and Agrarian Reform (INCRA) issued 154 titles to 217 Afro-Brazilian communities and 13,145 *Quilombola* families; these titles correspond to approximately one million hectares. This figure is very low considering the titling law is almost 30 years old and there are more than 4,500 black communities waiting to have their ancestral territories officially recognized. Figure 13.9 shows legally-recognized Afro-descendant communities in Brazil (Fiabani 1988; De-Torre 2018).

13.10.1.2 Colombia

The period after the abolition of slavery is considered the transition of Afro-Colombian people towards the classic notion of "peasantry." In the 1960s, Afro-descendant Indigenous movements began to question rural policies that grouped them within the group of creole people, following early 20th century legislation enacted so that their racial lines would be physically whitewashed and diluted through miscegenation (Ulloa 2007; Castro-Gómez 2009; Oliva 2017). Different violent and extractive boom periods in the Amazon have promoted internal migration of Afro-Colombians mainly from the Pacific region to the Amazon (Trujillo Quintero 2014; Kothari et al. 2018), where these populations are becoming more visible (Acosta Romero 2019). Since the enactment of the 1991 constitution, Indigenous and Afro peoples in Colombia have the right to citizenship. The collective character of their ancestral territories and the authority of these peoples within these territories is recognized. From this historical milestone, the Afro-Colombian communities of the Pacific began processes to claim these rights. Afro communities in other regions of the country are becoming increasingly visible. Previously, both Afro communities and Indigenous peoples were considered a part of the demographic category of peasants. Recently, some Colombian universities have started to study Afro-Amazonians and there is an increasing number of NGOs interested in carrying out projects and programs with this population group.

Along the Pacific forest region, there are 6 million titled hectares of collective territories of Afro-descendant communities. The Amazon was the center of Colombia's civil conflict, and these territories are a testament to the experiences of Afro communities trying to protect their land in the midst of an armed conflict. The permanent presence of armed groups, drug trafficking, and mining have generated devastation, massive forced displacement, massacres, recruitment of youth, hostility among civil society, and anxiety (Escobar 2015; Martínez and Tamayo 2016; Nocua Caro 2019). In addition, oil palm plantations are expanding at the expense of Colombian Pacific forests (Carney 2020 p. 17). Following the 2016 peace accords between the Colombian government and the FARC, one year of tranquility was followed by rapid investments in resource extraction, which may result not only in unsustainable resource use, but also in violence towards Indigenous and Afro-descendant peoples.

13.11 Conclusion

Using both a cultural exchange approach and a socio-historical environmental perspective, this chapter illustrates overlooked issues concerning the descendants of Africans in tropical regions in the Americas, including the Amazon. These approaches allow for the identification of both research gaps and aspects for nurturing policy frameworks for natural resource conservation and the community well-being strategies of Afro-descendant people. First, studies on the contribution of African peoples to the Americas have traditionally focused on cultural aspects such as music or sports (Cordova 2019). One of the neglected aspects has been the fact that African enslaved people arrived in the Americas from tropical regions where the domestication of species, agriculture, and ecosystem management had already been in place for millennia. Tropical origin was an advantage for enslaved Africans in the Americas. The ability to manage African biodiversity and highly complex ecosystems helped enslaved people adapt to the extreme situation they faced. These skills must have played an essential role in their strategies to maintain resilience in the face of hostile environments, either working on plantations or living in the middle of the forest as Maroons fleeing slave masters. These abilities could have contributed to the adaptation of many species of flora and fauna to the Americas, species remain a part of the region's food, culture, and economy. Slave ships

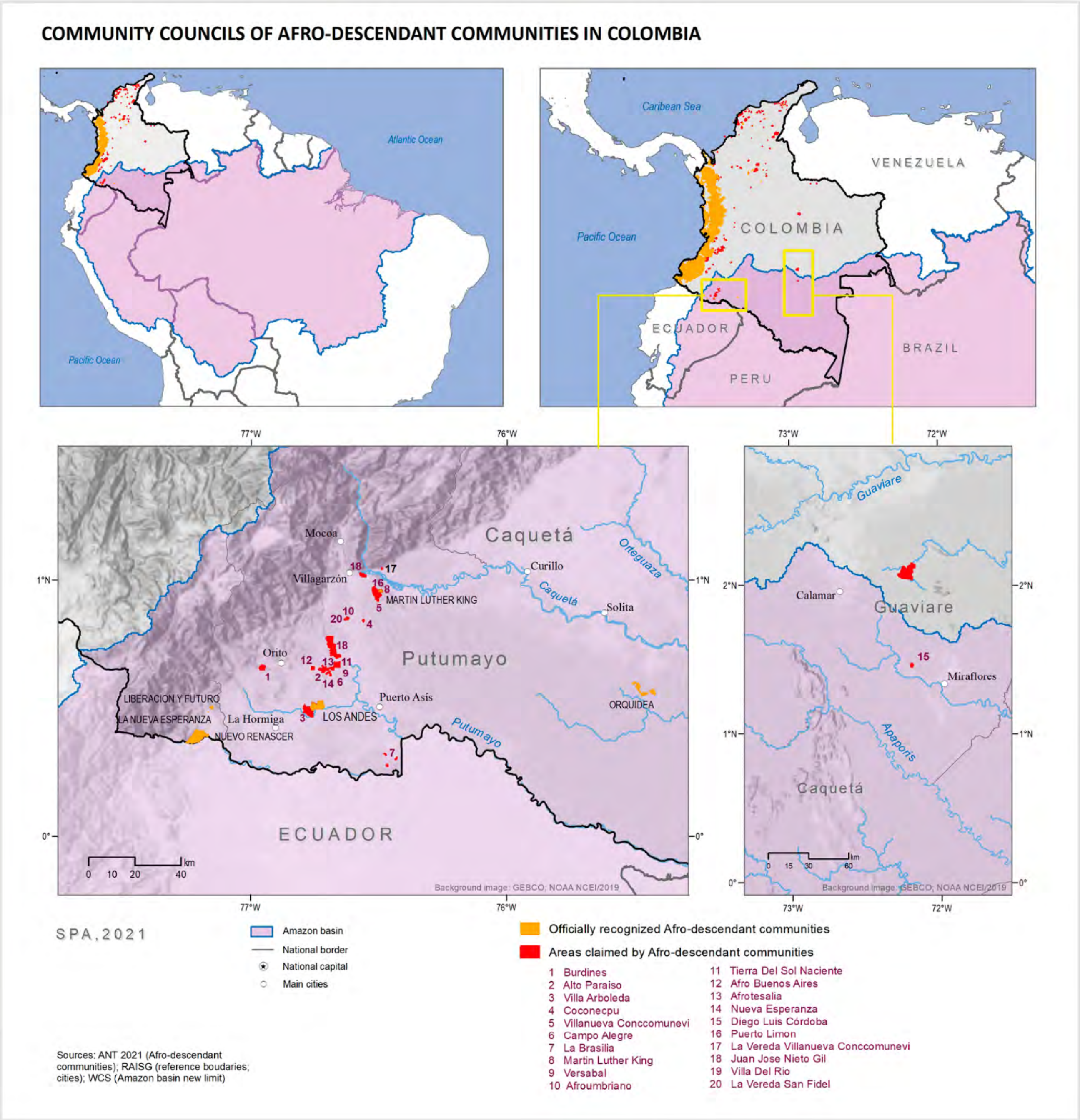


Figure 13.10 This map shows legally recognized territories of Afro-descendant communities in Colombia. Throughout the forest of the Pacific region, there are 6 million entitled hectares. The 1991 Colombian Constitution legitimized the entitling process. Afro-descendant communities in the Amazon are following the path of communities from the Pacific in exercising civil rights and ethnic governance of ancestrally occupied territories. Sources WCS-Venticinque *et al.* (2016), RAISG (2020), Agencia Nacional de Tierras ANT (2020).

played an important role in the transportation of genetic resources in the form of food for the Atlantic journey, facilitating the exchange of many species between the continents. Ships also transported enslaved peoples' knowledge, beliefs, and practices central to the adaptation of species for agriculture and livestock in the Americas (Carney and Rosomoff 2009). Gaps in research remain, including the strategies African peoples adopted for their own adaptation, survival, and economy during both slavery and liberation (Carney and Voeks 2003; Van Andel 2010; Vossen *et al.* 2014; De-Torre 2018; Carney 2020). Researchers agree on the role of Africans in the positive transformation of the landscapes of the tropical Americas (Leal 2004; Leal and Van Ausdal 2014). There is another neglected aspect that may have influenced research on African people in the Amazon. Most of the body of knowledge, particularly that constructed in the Amazon about African descent, has taken place in non-Spanish speaking countries (Oliva 2017).

There are arguably geographic, economic, and sociological reasons for the historical invisibility of African descendants in Latin American countries. On the one hand, a geographical explanation is related to the places and ports where enslaved people disembarked in South America. Although the history of Iberian colonization reports early the presence of enslaved African Indigenous Peoples in the Amazon, arrival followed different patterns in Spanish and Portuguese colonies. The Portuguese strategically founded ports, economic enclaves, and cities at the gates of the Amazon. Therefore, colonial society in the Brazilian Amazon had a broad relationship with enslaved Africans. Besides, this empire had supremacy of the slave trade. Not surprisingly, Brazil is the Latin American country with the largest Afro-descendant population. The Spanish Empire founded the main cities and central economic enclaves from the Andes to the west towards the oceans. Therefore, there was a greater demand for enslaved people in agricultural production and domestic servitude for mainstream society in this geographical portion. In the case of the western region of South America, reaching the Amazon requires crossing the Andes mountain range. The regions to the east of the Andes were considered wild and the refuge of savages, Maroons, bandits and outlaws. Extractive enclaves were established in the Amazon that motivated waves of colonization at different times in history. Enslaved people established Maroon societies in the western Amazon and played central roles in the history of the basin.

On the other hand, the sociological explanation for the invisibility of African descent in the Amazon basin is associated with deterministic constructs and stereotypes that revolve around the African presence in the Americas. The *first* sociological construct is the idea that Afro-descendant peoples have only contributed unskilled, heavy labor, which is connected to stereotypes about their strength and stamina (De Friedemann and Arocha 1986; Wood 1996; Carney 1996, 2009). The *second* construct is the "spatial notion of culture" characteristic of some anthropological approaches (Maya 1998; Castro-Gómez 2010 p. 28), which identifies specific human groups with certain geographic regions. The perception is that Afro peoples are only found in coastal regions and certain places in the Andes. There is also the notion of African savagery, with which the enslaved arrived in the Americas. The *third* construct is the ideal of whiteness in Latin American society, which began during the Enlightenment. In this period, botanical expeditions considered European knowledge superior and the knowledge of Indigenous Peoples and African descent groups as a superstitious Doxa that deceived the senses (Castro-Gómez 2010). A *fourth* construct involves the relationship of Latin American societies with nature, the forest, and its inhabitants. These are considered unproductive lands, and the savages that inhabit them lazy and unable to convert them to productive areas. Finally, both Afro and Indigenous peoples in the Americas are considered peoples without their own history, and without the capacity for action (Granero 1992).

The history of peoples of African origin during their enslavement and subsequent liberation shows ways to strengthen resilience and navigate uncertainties. Access to environments that other segments of the population view with apprehension and disdain have allowed African descent people to adapt, maintain livelihoods and health, and exercise their belief systems. These are strategies that offer keys to wellness and conservation. The dynamic relation between the rainforest, rural areas, and urban centers and markets allows Afro families to have a diversity of livelihood strategies and therefore maintain economic resilience.

This chapter does not intend to delve into the invisibility of Afro groups in national statistics and welfare policies or in the violation of their civil and human rights in the different countries of the basin. This is being done very well by academics throughout the region, including Afro-Latin American scholars (Buffa 2008; Lechini 2008; Oliva 2017). This chapter wants to raise awareness of a group traditionally neglected by science and its contribution to the conservation of tropical regions of the Americas. Prominent Latin American scholars assert that ignoring Afro-descendants in scientific research on social, cultural, and historical aspects of Ibero-American countries is an incomplete task. This chapter adds to this statement the need to include this community in research topics such as agriculture and agroecology and ecosystem and biodiversity management. The latter themes are a hinge to integrate disciplines in research on the contribution of the African descent people to the economy and well-being of the Americas.

Furthermore, academics have drawn attention to the importance of the adaptation strategies of Afro-descendants to tropical rainforests in the positive transformation of such landscapes in the Americas. However, complex agronomic arrangements in both domestic and agricultural systems, and agrobiodiversity and plant management practices that support polyculture food crops, are gradually being replaced by new waves of monoculture plantations. The history of African descent in the tropical and subtropical rainforests of the Americas provides clues for navigating uncertainties and strengthening the resilience of these groups. This history also shows possible paths to ensure the well-being of the formerly enslaved population and conservation at the same time. The titling of ancestral territories and self-determination are appropriate ways to initiate historical repairs and can restore the possibility for African descent people to find their own path. By way of conclusion, the mythology of the Akan people from Ghana shows African descent people in the Americas a path to navigate in diaspora: the Sankofa bird reminds people to look to the past in order to move forward to the future (Carney and Rosomoff 2009 p. 27).

13.12 Recommendations

- African origin populations have made a significant contribution to sustainable resource management practices in the Amazon. African enslaved people arrived in the Americas from tropical regions where they had managed ecosystems, engaged in agriculture, and domesticated species for millennia. This knowledge has contributed to positive transformations of tropical landscapes in the Americas.
- Consider Afro-descendant communities as strategic actors in the conservation of biodiversity, ecosystems, watersheds, tropical rainforests, and sustainable agriculture.
- Provide support to research vis-à-vis biodiversity, languages, ecosystem management, techniques, and environmental management practices in African descent community contexts.
- Include African descent populations in research endeavors, paying special attention to the Spanish-speaking countries where research is very incipient; these countries can learn from the research carried out in Suriname and Brazil.
- Research to inform conservation policy needs an interdisciplinary perspective that contributes to identifying and taking the contributions of African populations into account.
- An interdisciplinary approach in research should consider the differentiated perspective as a path to understand cultural diversity in the Amazon and design context-specific strategies for conservation (Ethnic-racial statistics and socio-cultural data).

- Deterministic doctrines and political Darwinian thought have influenced Latin America greatly. There is still a tendency in mainstream society to consider African descent and Indigenous Peoples as groups unable to make decisions. This influences environmental policy design and governance in Amazonian countries.
- Strategies to consider Afro-descendants and Indigenous peoples as central actors in decision-making should review the constitutions and legislation of Latin American countries for effective legitimation of inclusive actions.
- Learn from collaborative processes carried out between Afro-Amazonian communities and non-governmental actors who have established long-term relationships with local groups and the in-situ experience to accompany their processes.
- Support NGO initiatives that currently work with Afro communities, as well as women and youth groups in the Amazon.
- Promote the contributions of Afro-descendant communities to the Americas through education, policy, and media programs This can help to address long-term structural issues and stereotypes.
- African descendants face critical situations of violence and forced displacement, which not only violate their fundamental rights, but also disrupt sustainable tropical forest management systems. These groups have historically been absent from governmental programs and require strategic support.
- Support education programs on Afro-descendant communities in the countries of the basin, both for mainstream society and for the Afro-descendants themselves, including their history, contributions, and management of natural resources. This action contributes to the social and cultural internal strengthening process carried out by African descent organizations.

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