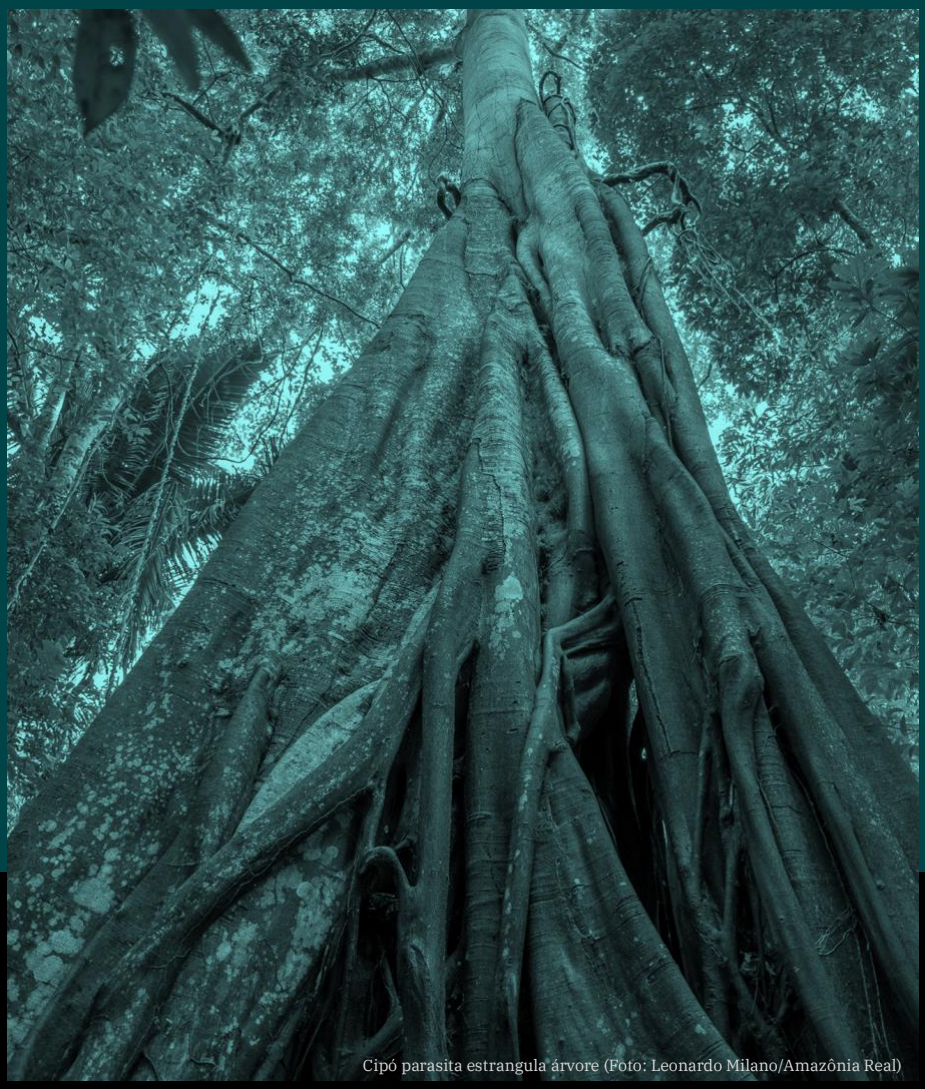
Amazon Assessment Report 2021

Chapter 4

Amazonian ecosystems and their ecological functions



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

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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INDEX

GRAPHICAL ABSTRACT **2**

KEY MESSAGES **3**

ABSTRACT **4**

4.1. AMAZONIAN ECOSYSTEMS: AN INTRODUCTION **4**

4.1.1. VEGETATION TYPES FROM THE HIGH ANDES TO THE ATLANTIC OCEAN 5

4.2. LOWLAND AMAZONIAN ECOSYSTEMS **7**

4.2.1 TERRESTRIAL ECOSYSTEMS 7

4.2.1.1 Lowland Rainforests *8*

4.2.1.2 White sand forests *10*

4.2.1.3. Savannas and grasslands *10*

4.2.2. FRESH WATER BODIES AND WETLANDS 12

4.2.2.1. Rivers, Lakes and Forest streams *12*

4.2.2.2. Freshwater Wetlands *16*

4.3. ECOSYSTEM FUNCTIONING **18**

4.3.1. PRIMARY PRODUCTIVITY, NUTRIENTS, FOREST DYNAMICS AND DECOMPOSITION 18

4.3.1.1. Terrestrial ecosystems *18*

4.3.1.2. Freshwater ecosystems *22*

4.3.2. THE FLOOD PULSE AND AQUATIC-TERRESTRIAL TRANSITION ZONE 23

4.4. CONCLUSIONS **25**

4.5. RECOMMENDATIONS **26**

5. REFERENCES **26**

Graphical Abstract

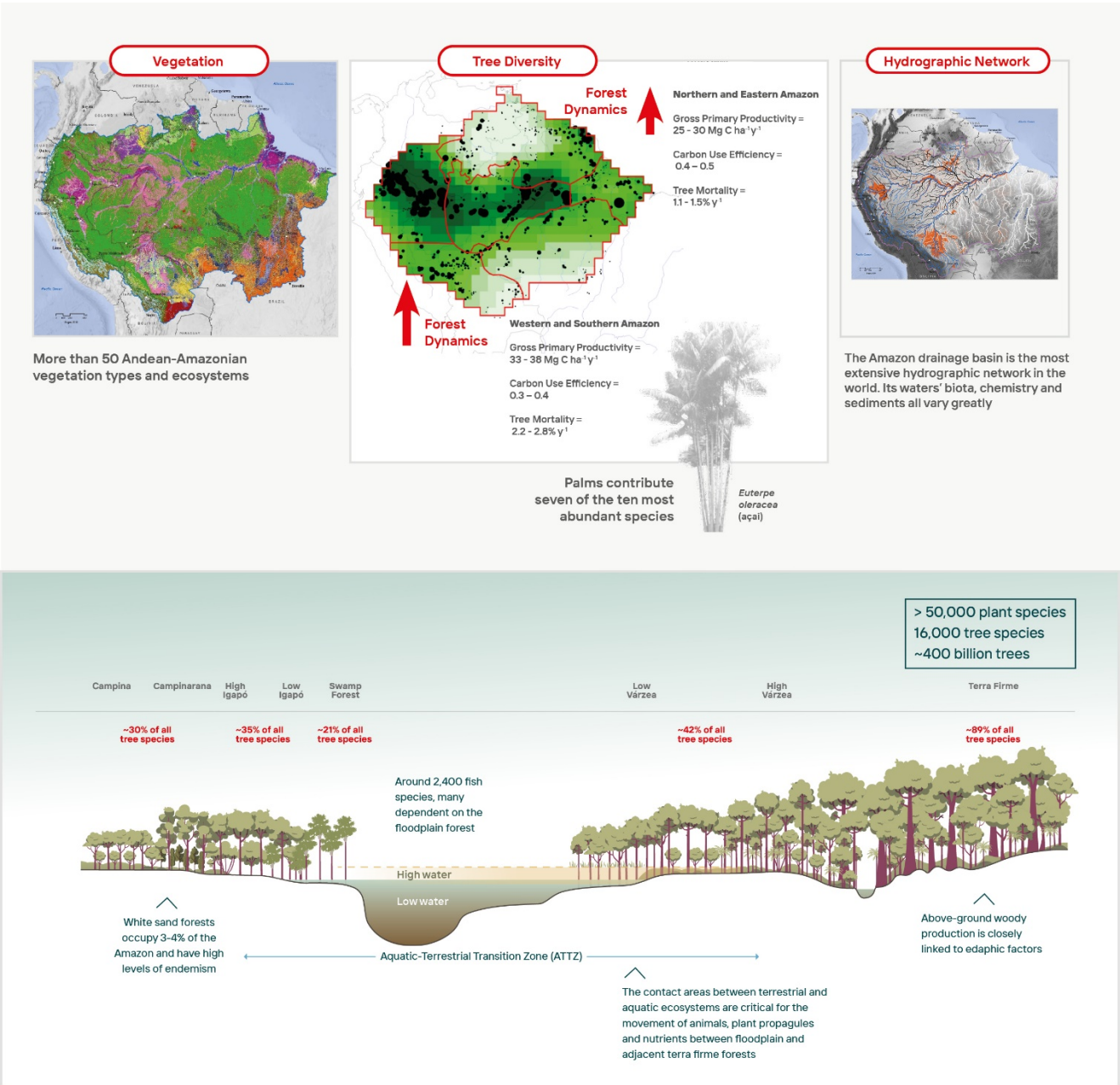

Figure 4A Graphical Abstract

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).

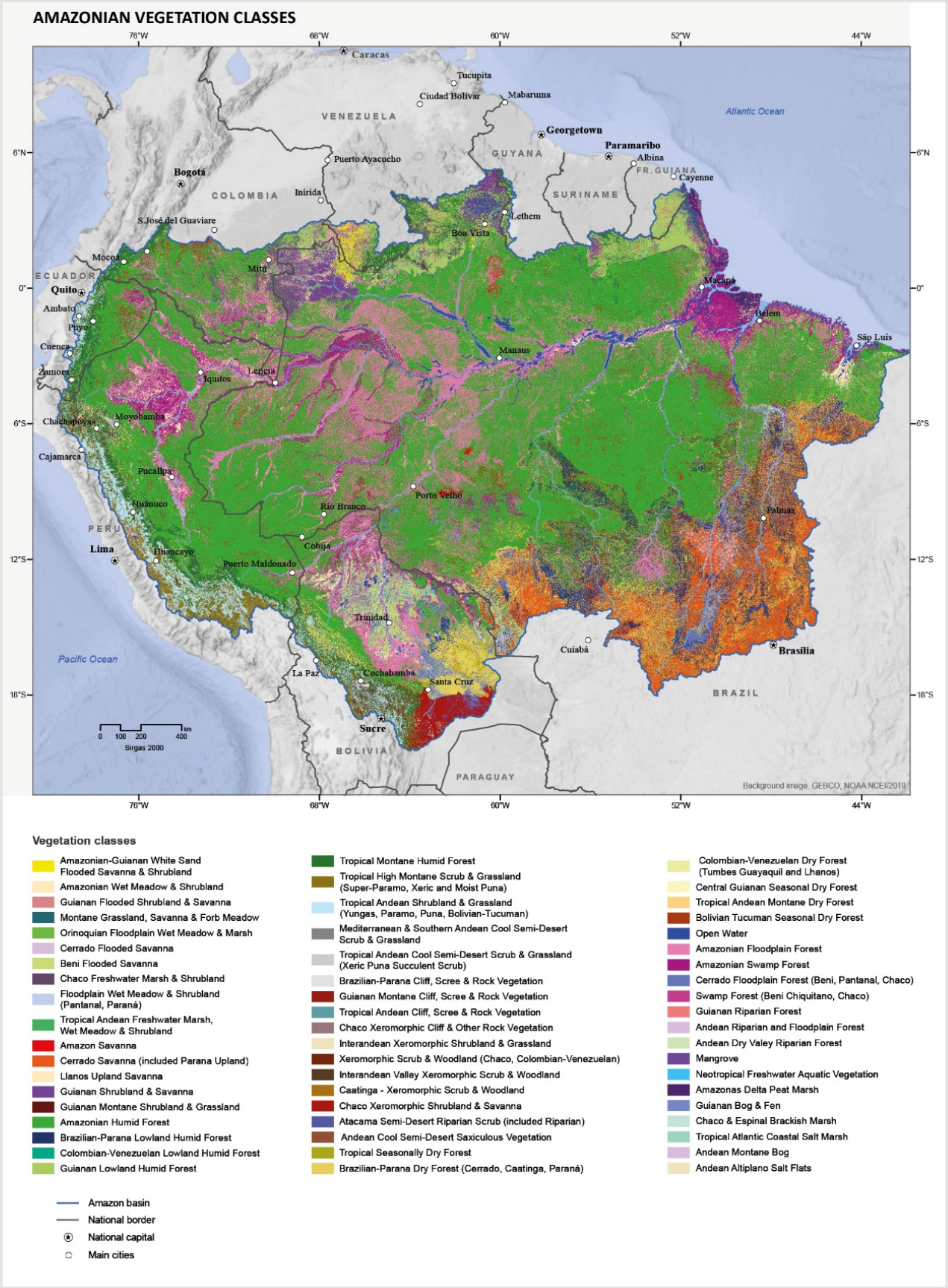

Figure 4.1 Map of Amazonian vegetation and ecosystems (Source: Comer *et al.* 2020). The solid gray box highlights the high richness of vegetation and ecosystems found in the latitudinal and altitudinal gradients in the Amazon (see Figure 4.4 for detail).

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

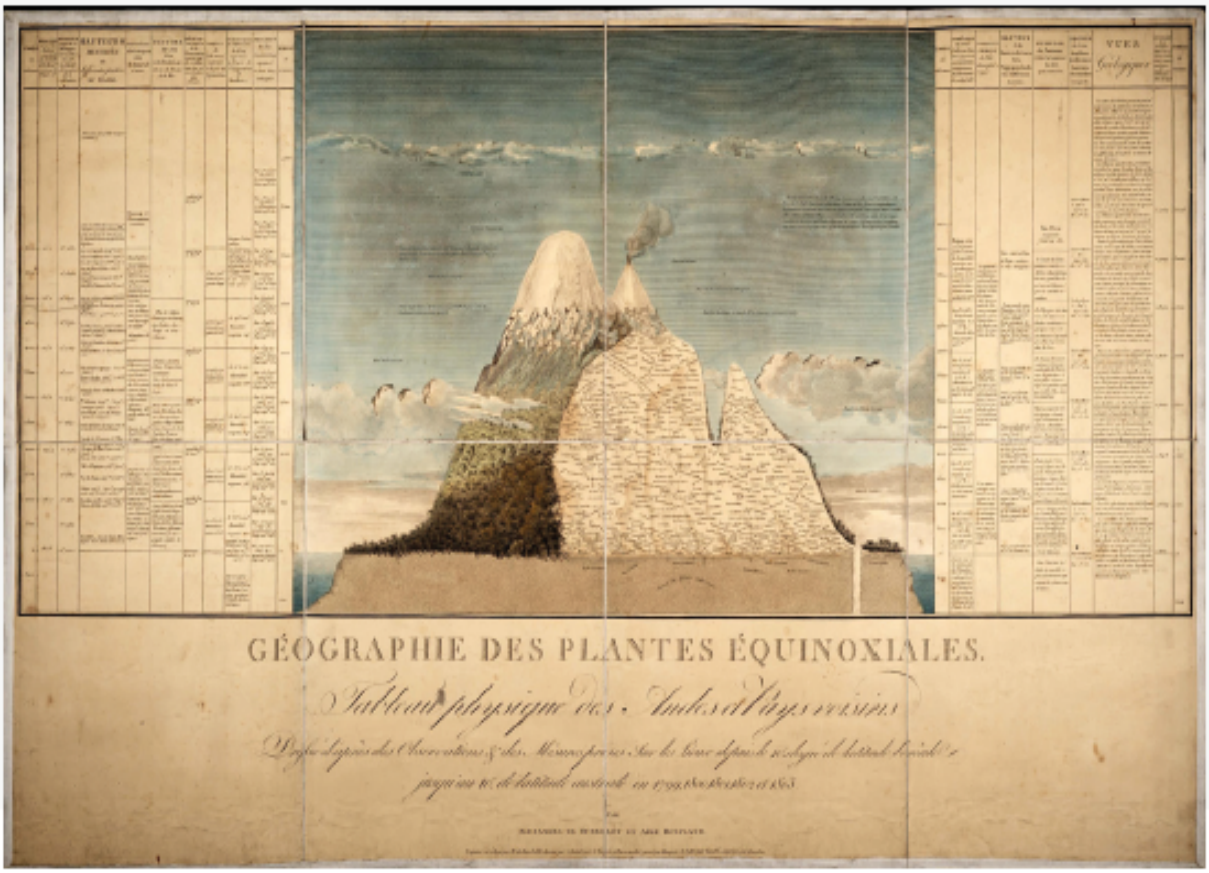

Figure 4.2 Alexander von Humboldt's *Tableau Physique* (Humboldt 1805), a graphic overview of plant communities, from the Pacific to the Atlantic Ocean and passing over the Andean mountains. Reproduced with permission from the Peter H. Raven Library at the Missouri Botanical Garden (https://www.biodiversitylibrary.org/page/9869921).

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).

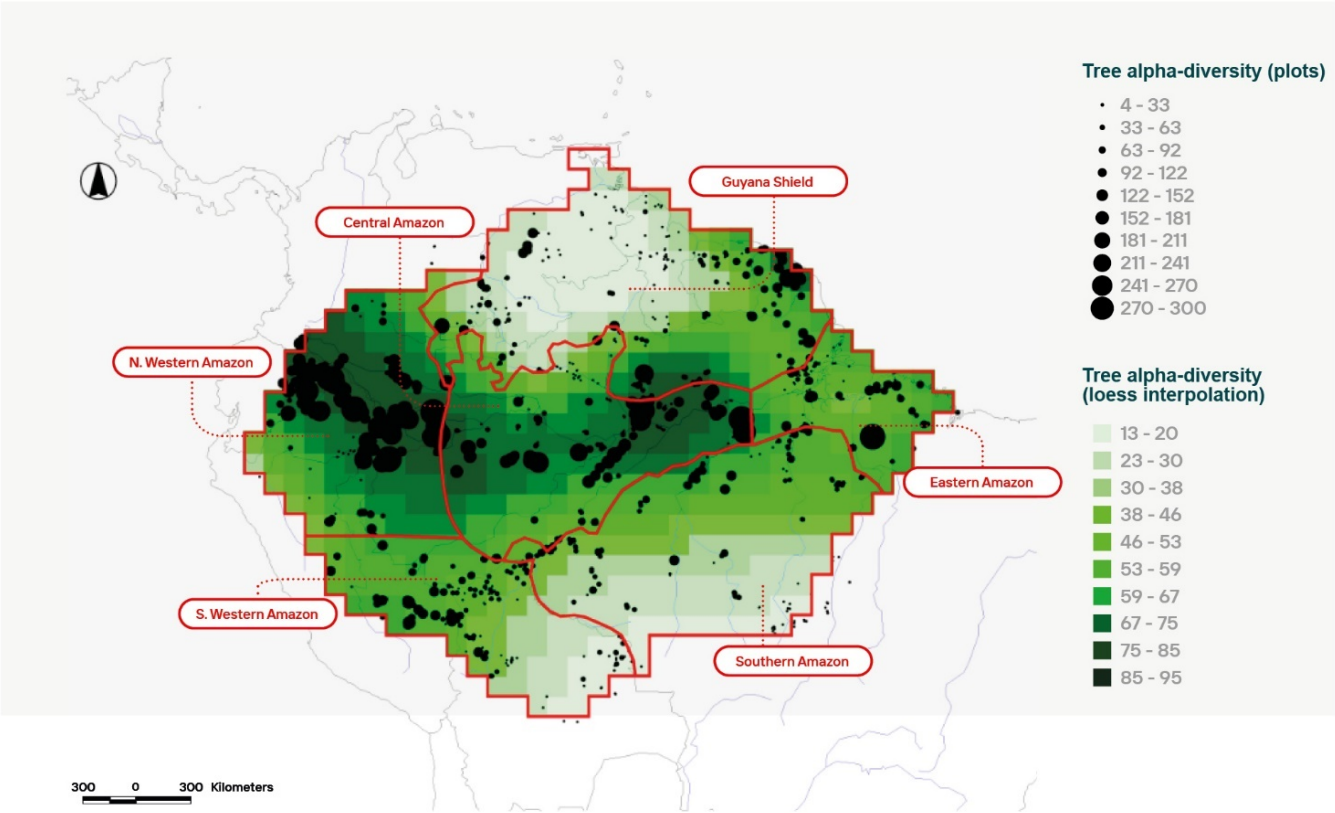

Figure 4.3 Map of tree α-diversity of the Amazon (http://atdn.myspecies.info), based on an interpolation of Fisher's α of 2,282 plots of mostly 1-ha. Black dots: Fisher's α of individual plots. Green background color: the interpolated values calculated for 565 Amazonian 1-degree grid cells (~111 km). 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

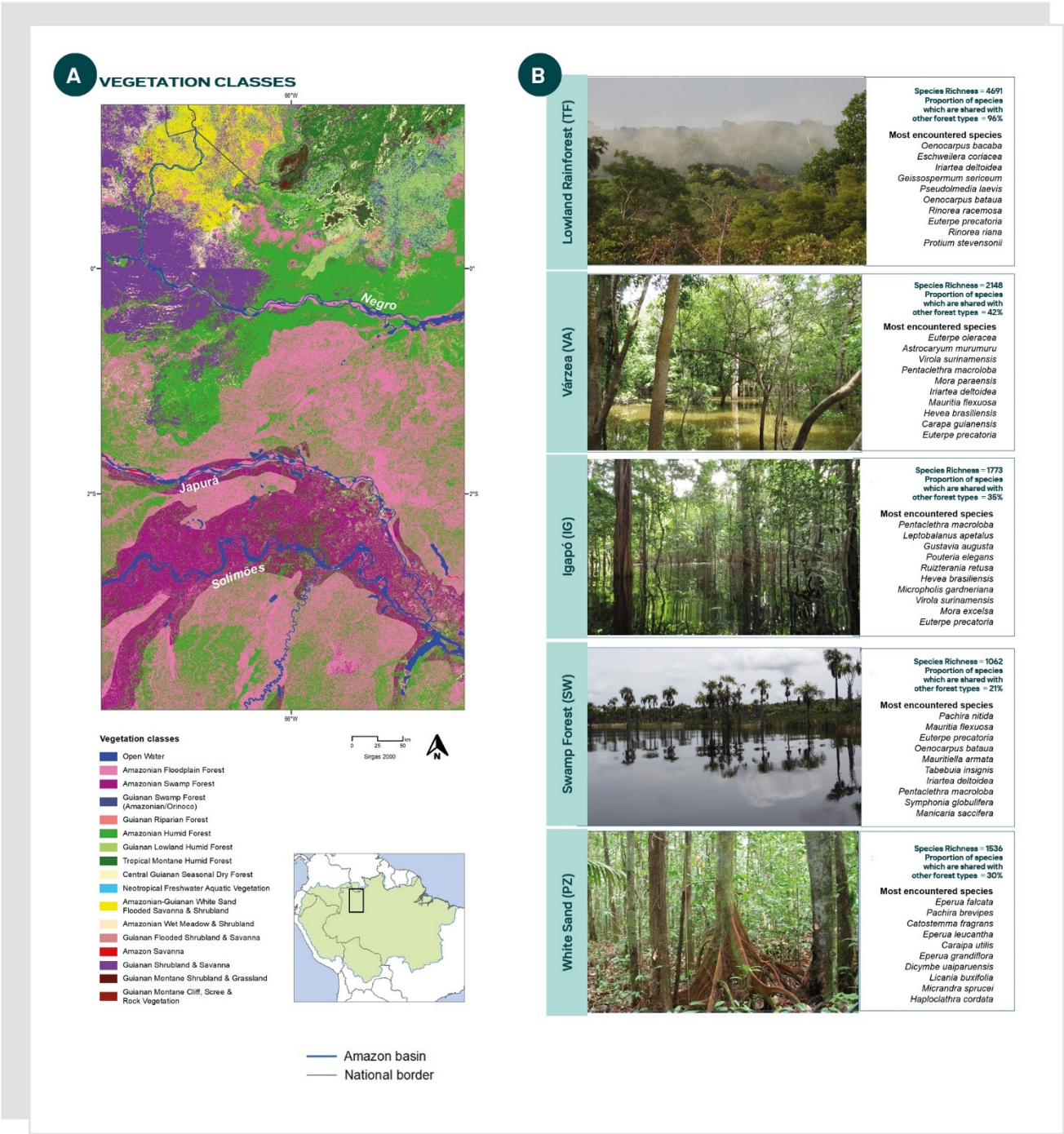

Figure 4.4 A. Key ecosystems are found in Amazonian lowland rainforests, such as floodplain forests, Amazon savanna, white-sand savanna, and seasonally dry forest. B. The ten most encountered tree species on ~2,000 plots across the Amazon by forest type (IG – igapó, PZ – white sand forest, SW – swamp 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

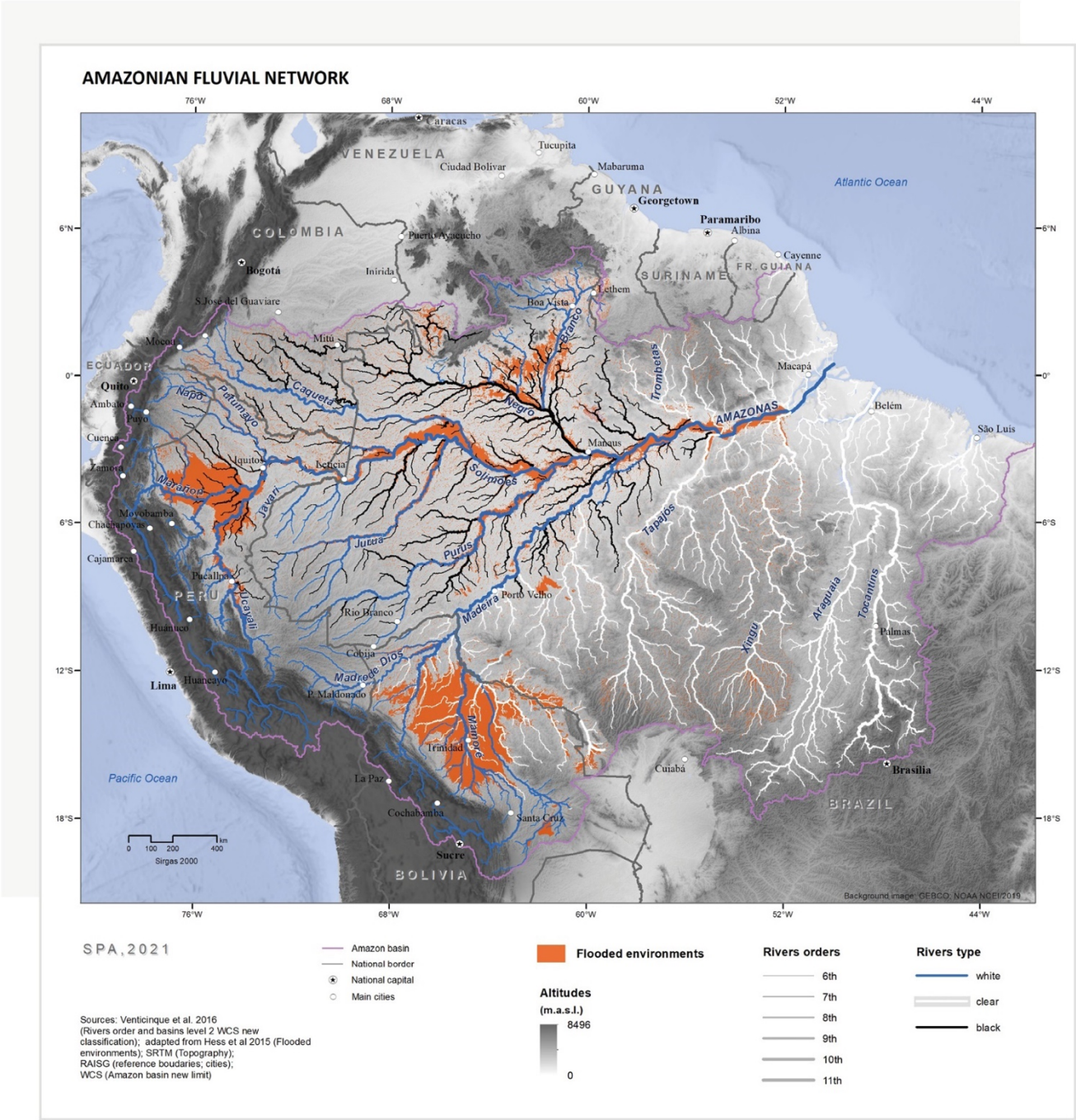

Figure 4.5 Amazon River Network across the largest tributary systems and the entire Amazon Basin (source: Venticinque et al. 2016), indicating the distribution of flooded environments (modified from Hess et al. 2015). Wetland areas cover ~14 % of the basin (nor considering Tocantins-Araguaia drainage 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) Hitchock[1]	100	12
Monospecific stands of *Paspalum fasciculatum* Willd.[2]	70	7.7
Mixed populations dominated by *Hymenachne amplexicaulis* (Ruudge) Nees[2]	48	9.5
Monospecific stands of *Paspalum repens* P.J. Bergius[2]	33	4
Monospecific stands of *Oryza perennis* Moench[2]	27	4
Mixed populations dominated by *Oryza perennis* Moench[2]	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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