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)

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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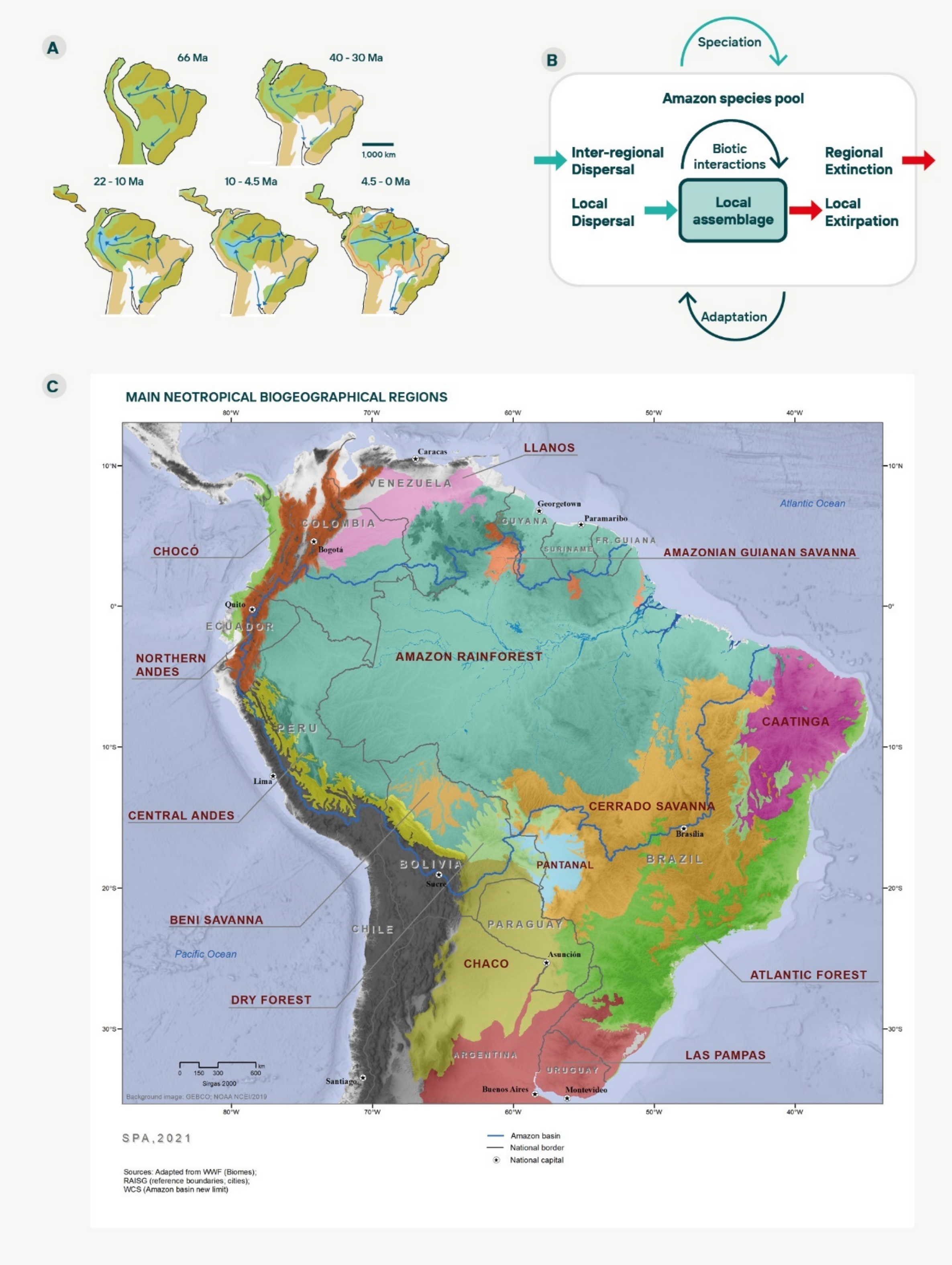
Graphical Abstract



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

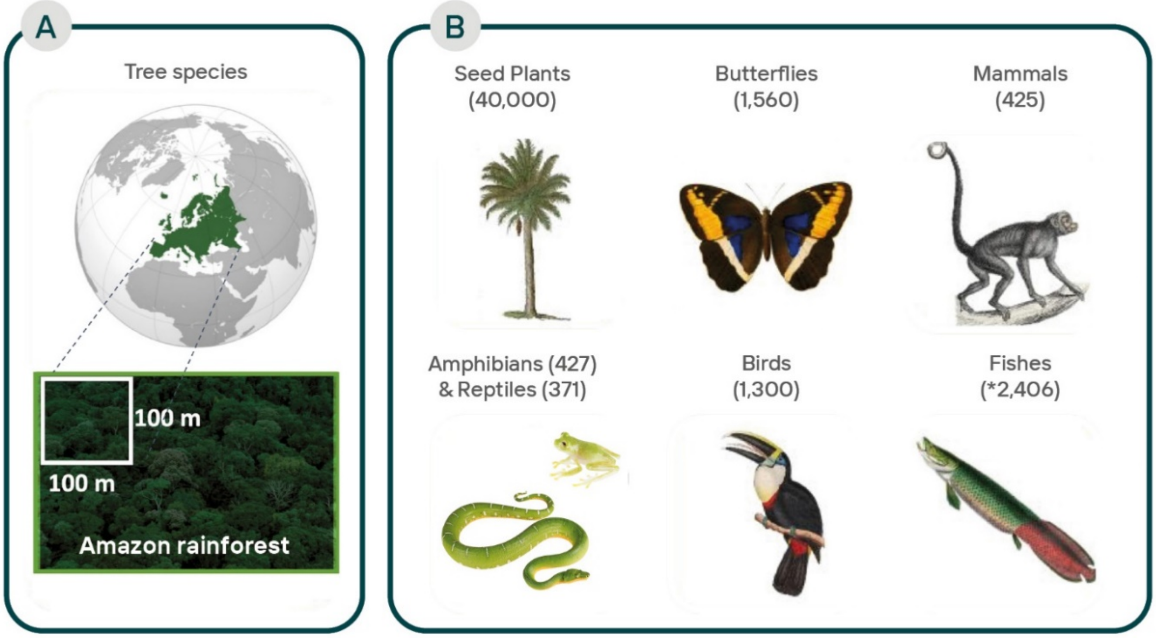


Figure 2.2. The Amazonian lowlands in numbers (minimum estimates based on current knowledge). A. More trees species are found in a 10,000 m^2 area of Amazon rainforest than in the whole of Europe (Ter Steege *et al.* 2006). B. Estimated numbers of species of selected Amazonian lineages, including vascular 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).

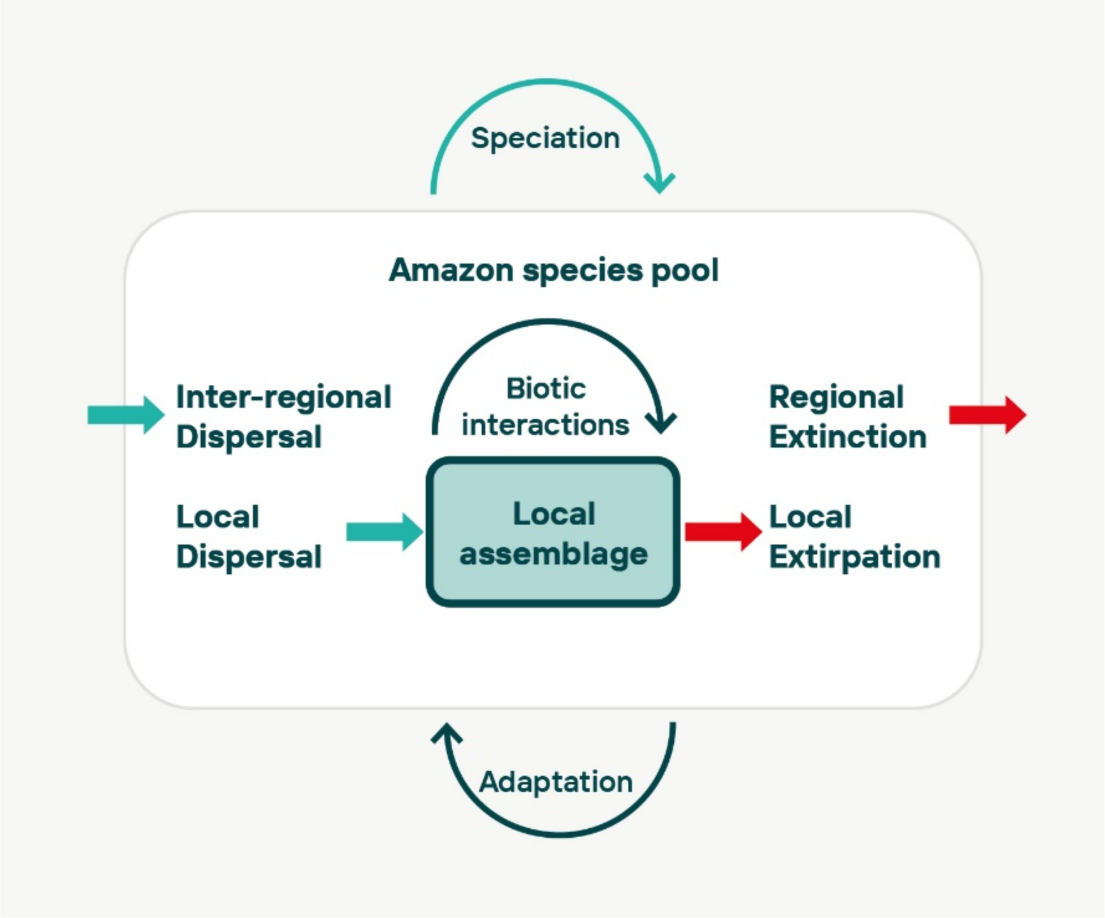


Figure 2.4 Regional and local processes underlying the assembly of the Amazonian biota. The regional species pool (outer light-blue box) is defined as the sum of all the local species assemblages (inner dark-blue box). Blue arrows indicate processes that increase species richness, red arrows highlight 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).

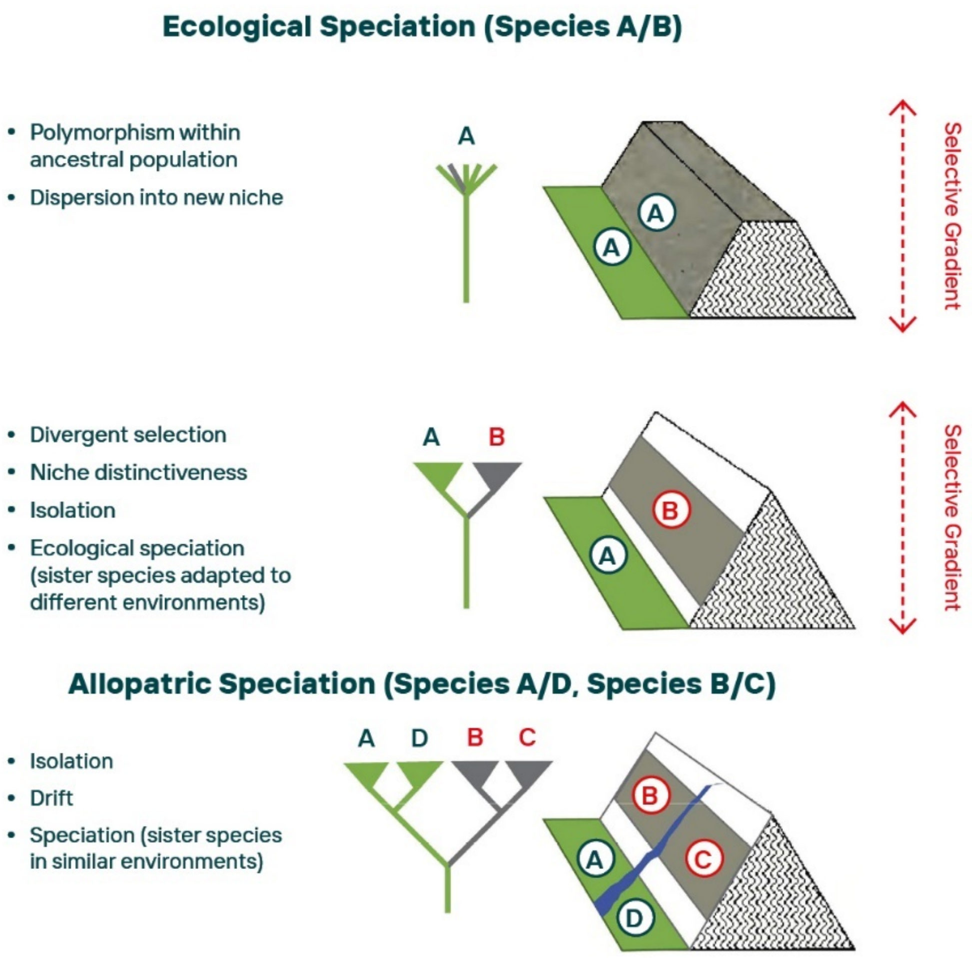


Figure 2.5 Common speciation mechanisms in the Amazon and elsewhere. Ecological speciation: the process by which new species form as a consequence of selection along climatic or ecological gradients, such as those encountered in the Andes. Note that the resulting species occupy distinct environments. 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

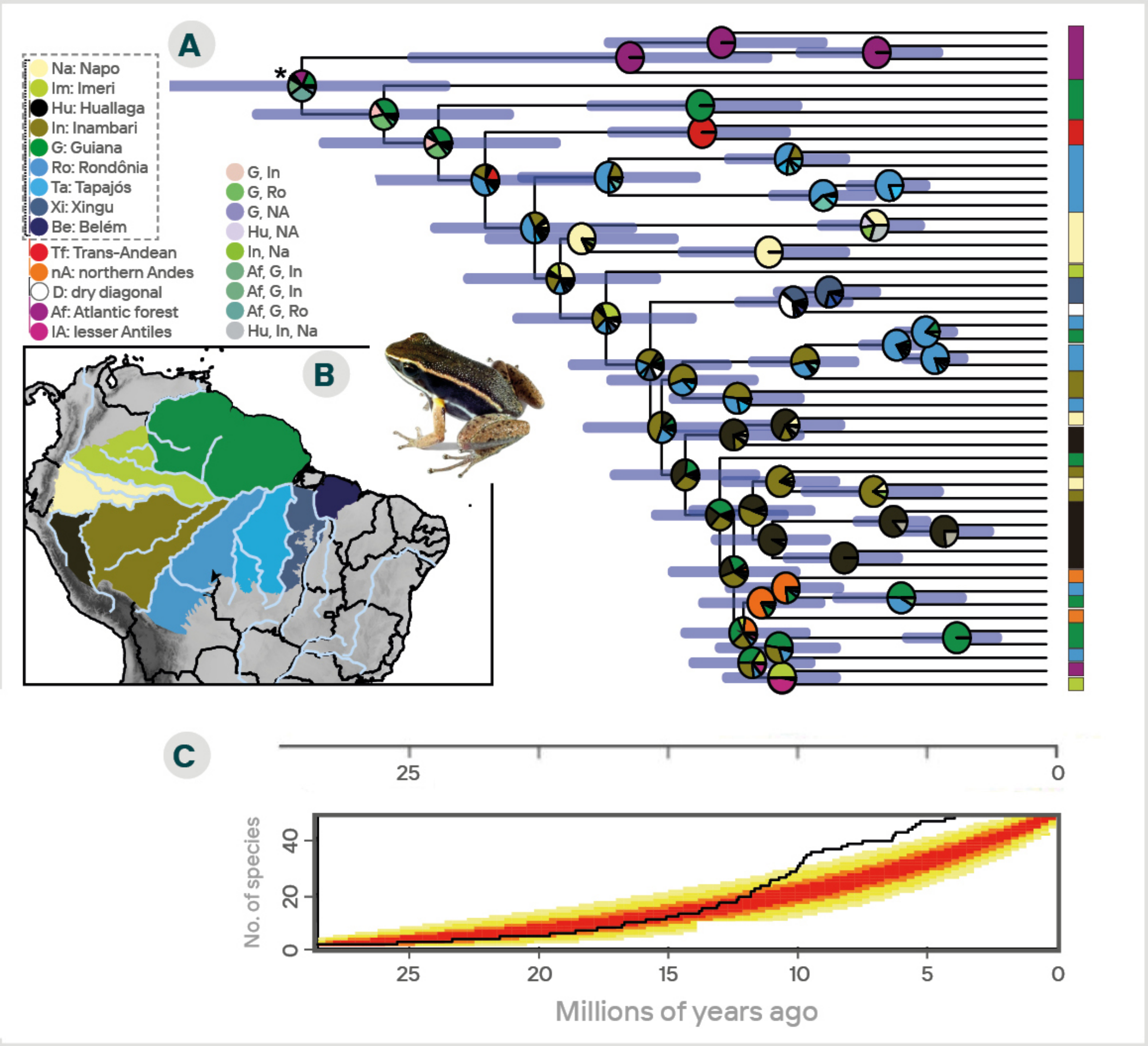


Figure 2.6 Diversification and endemism in Amazonian rocket frogs (*Allobates* spp.). Closely related species display an allopatric pattern of distribution, matching interfluves delimited by modern Amazonian rivers. (A) Evolutionary relationships, represented as a phylogenetic tree. Time is provided 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).

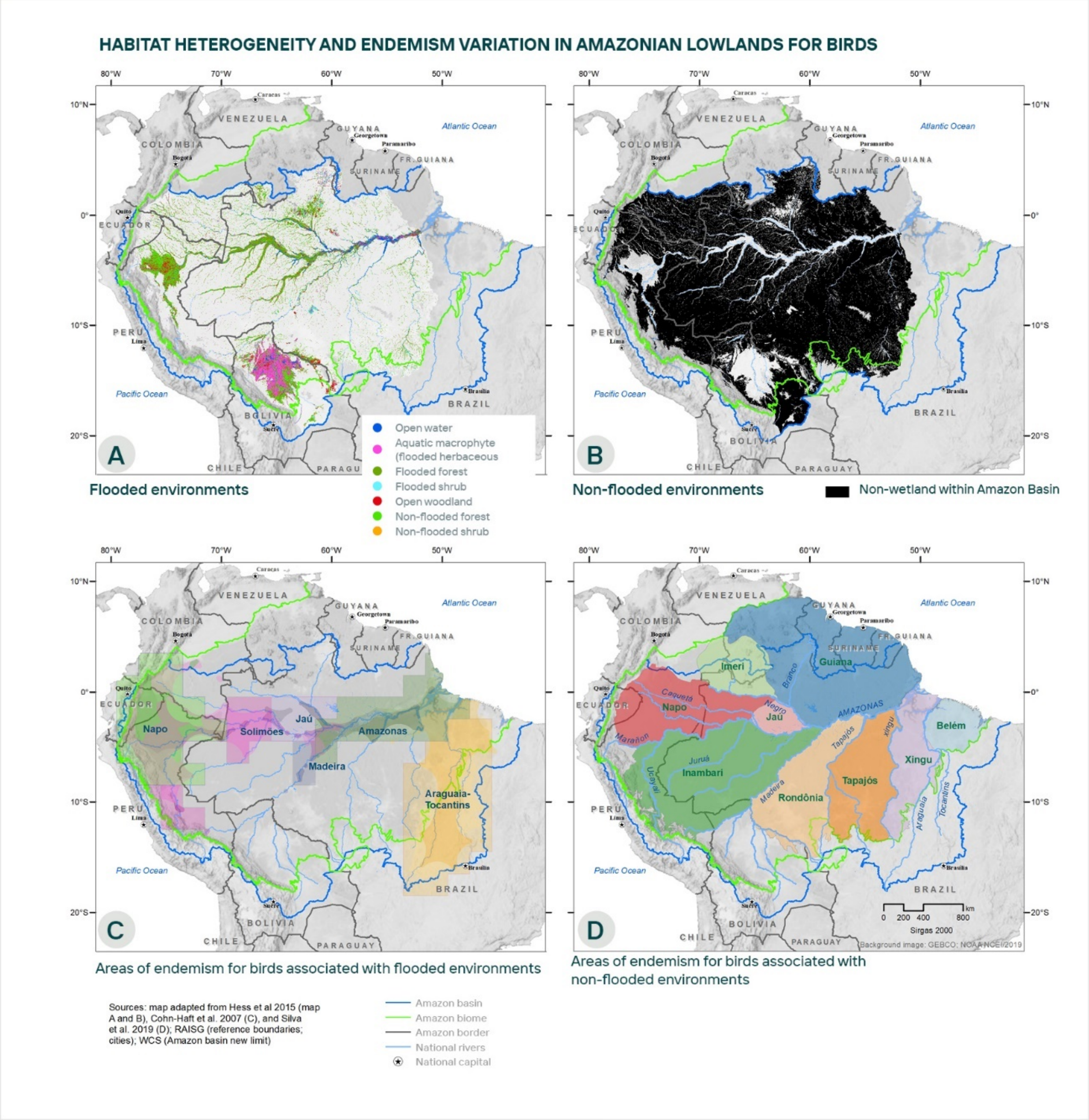
Habitat heterogeneity has played an important role in the formation of Amazonian biodiversity, with geological changes also impacting the ecological conditions available to the Amazonian biota. Andean uplift, for instance, has had a major effect on the Neotropical climate; it created both habitat and 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.

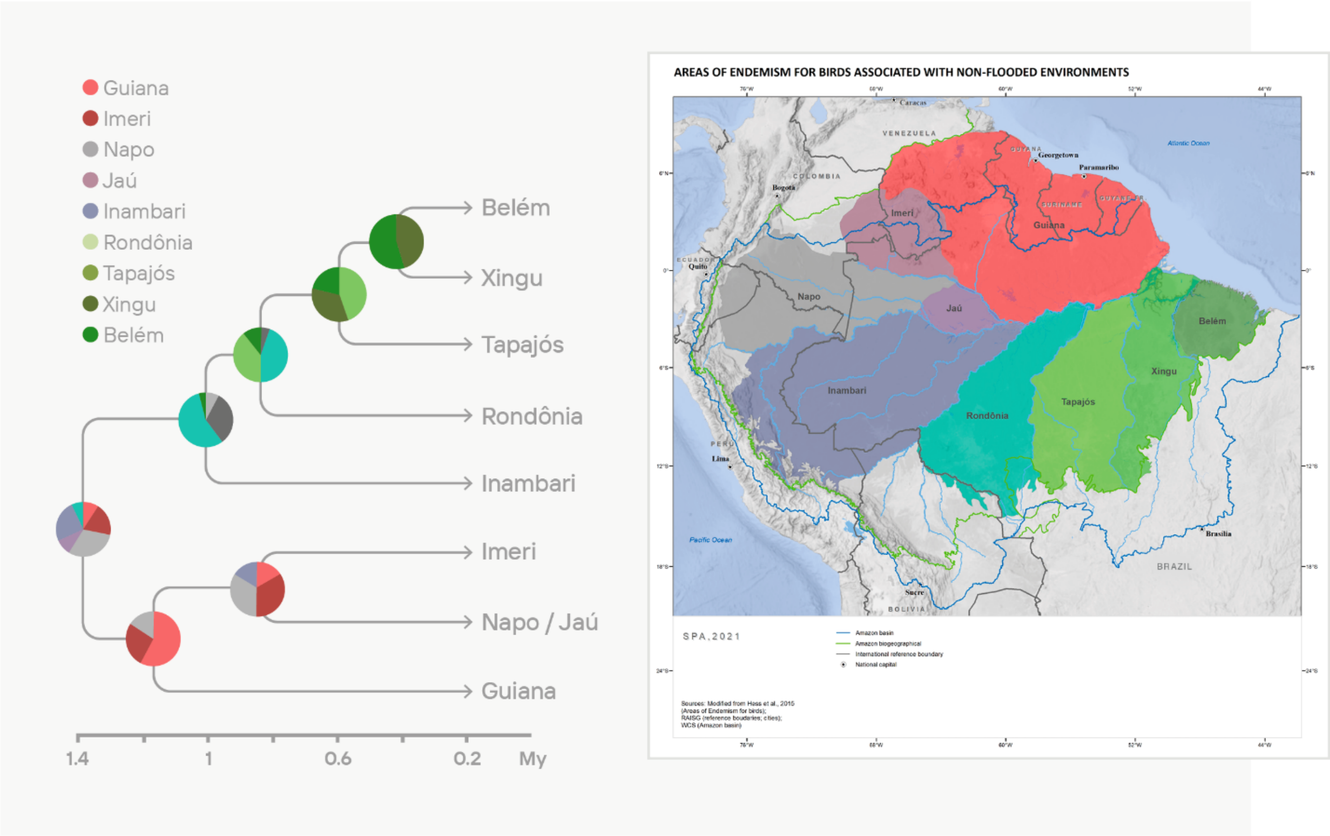


Figure 2.8 Summary of diversification patterns for 21 taxonomic clades of Amazonian birds restricted to the upland forest (*terra firme*) understory. Left: Relationships among nine areas of endemism, inferred from genetic data; pie charts denote ancestral area probabilities. Right: Areas of endemism 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).

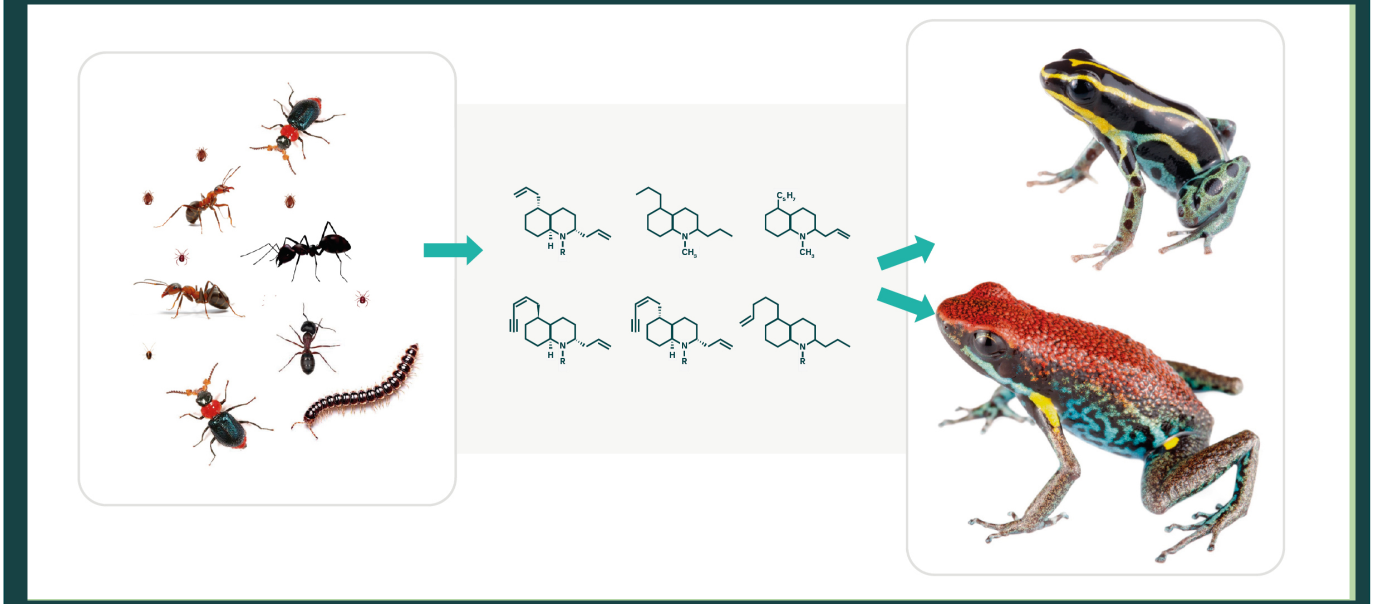


Figure B2.2.1 Poison dart frogs are protected by alkaloids that they sequester from their prey, including ants, mites, millipedes, and melyrid beetles (see Saporito *et al.* 2011 and references therein).

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

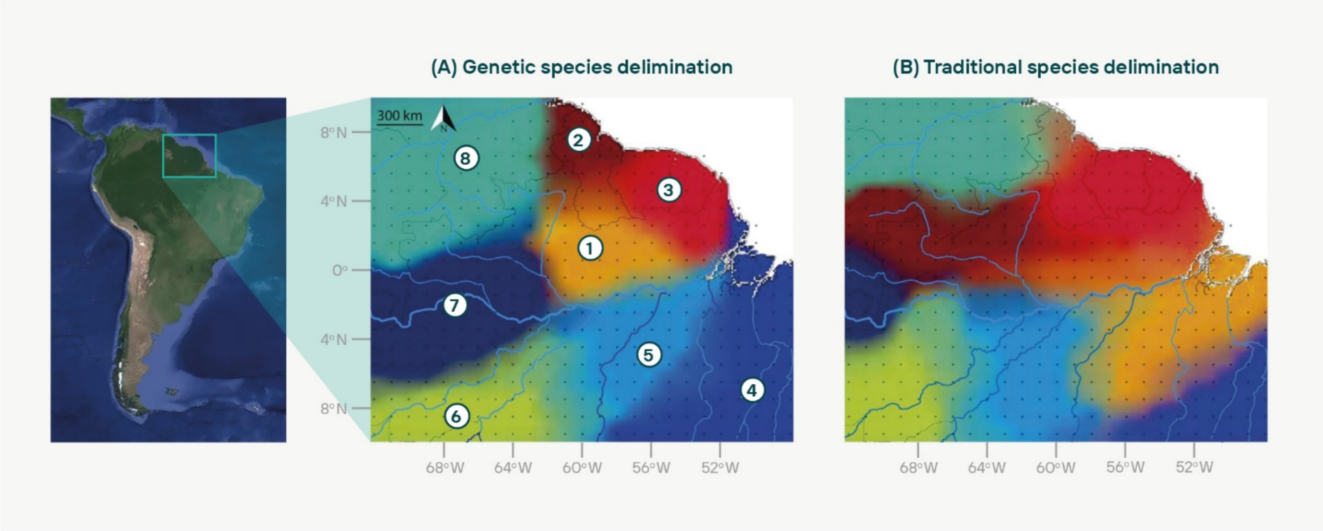


Figure 2.10 Bioregionalization based on species occurrence data for frogs in the eastern Amazon. A. Data from DNA-based species delimitation. B. Data from morphology-based taxonomy. Colors represent affiliations of cells to bioregions. Note both the bioregion boundaries and numbers of endemic species 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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