Science Panel for the Amazon (SPA)

Working Group 1

GEOLOGY AND EVOLUTION OF THE AMAZON REGION

Lead Authors: Juan M. Guayasamin and Carina Hoorn

CHAPTER 2: EVOLUTION OF AMAZONIAN BIODIVERSITY

Lead Authors of Chapter: Juan M. Guayasamin

Contributing Authors (Alphabetic Order): James S. Albert, Ana Carolina Carnaval, Juan D. Carrillo, Juan M. Guayasamin, Carina Hoorn, Lúcia G. Lohmann, Camila C. Ribas, Douglas Riff, Carmen Ulloa Ulloa,

CHAPTER 2

EVOLUTION OF AMAZONIAN BIODIVERSITY

Juan M. Guayasamin[1], Camila C. Ribas[2], Ana Carolina Carnaval[3], Juan D. Carrillo[4], Carina Hoorn[5], Lúcia G. Lohmann[6], Douglas Riff[7], Carmen Ulloa Ulloa[8], & James S. Albert[9].

---

[1] *Universidad San Francisco de Quito (USFQ), Instituto Biósfera-USFQ, Colegio de Ciencias Biológicas y Ambientales COCIBA, Laboratorio de Biología Evolutiva, campus Cumbayá, Quito, Ecuador.*

[2] *Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil*

[3] *Biology Department, City College of New York, and The Ph.D. Program in Biology, The Graduate Center of CUNY, U.S.A*

[4] *CR2P, Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, 75005 Paris, France.*

[5] *Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, 1090 GE Amsterdam, The Netherlands.*

[6] *Universidade de São Paulo, Instituto de Biociências, Departamento de Botânica, São Paulo, SP, Brazil.*

[7] *Universidade Federal de Uberlândia, Instituto de Biologia, Laboratório de Paleontologia, Uberlândia, Minas Gerais, Brazil.*

[8] *Missouri Botanical Garden, St. Louis, Missouri, U.S.A.*

[9] *Department of Biology, University of Louisiana at Lafayette, Lafayette, Louisiana 70503, U.S.A.*

INDEX

ACRONYMS AND ABBREVIATIONS

ca. = *circa* (approximately)

cal. yr bp = calibrated years before present.

CT = computed tomography

DNA = deoxyribonucleic acid

e.g. = for example

GABI = Great American Biotic Interchange

i.e. = that is

K-Pg = Cretaceous–Paleogene boundary, produced by an asteroid impact 66 million years ago that resulted in sudden mass extinction of species on Earth.

kg = kilograms

Ma = Million of years ago

m = meters

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. Biodiversity patterns (e.g., richness, endemicity) are oftentimes idiosyncratic to certain taxonomic groups and should not be generalized.
- Amazonian biodiversity accumulated incrementally over a period of 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 intact and most diverse set of terrestrial ecosystems on Earth.
- Amazonian species interactions are extraordinarily complex, and increasingly imperilled in the face of the immense and accelerating human-caused environmental changes.

Key message from this chapter:

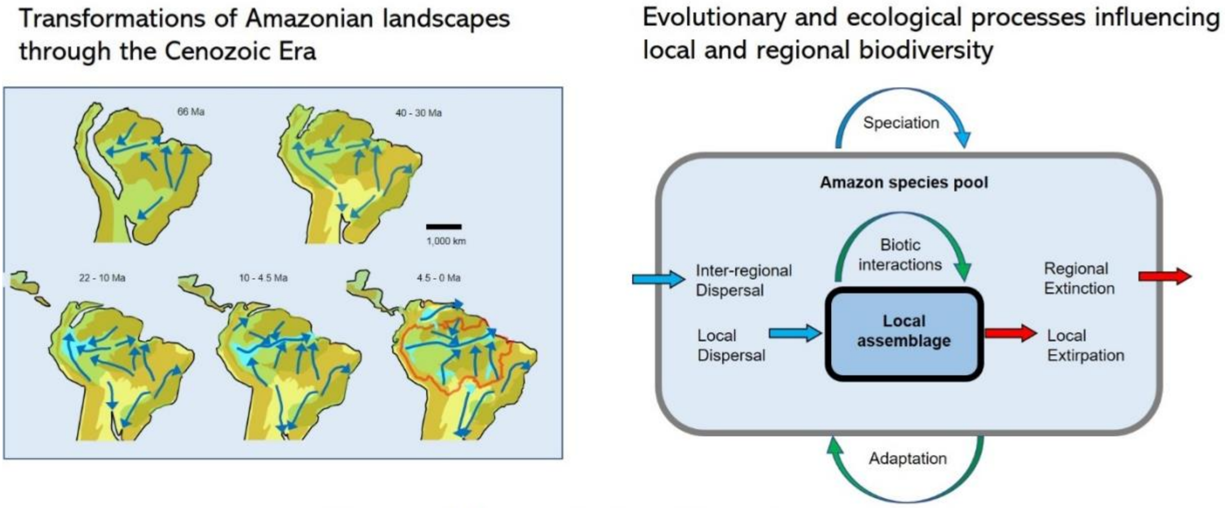
Amazonian biodiversity resulted from a long and dynamic history of environmental changes and biological interactions operating over millions of years. The persistence of the evolutionary and ecological processes that result in organismal diversification and adaptation is fundamental for the survival of this ecosystem, and for its critical ecological and economic functions for the region and for global society.

ABSTRACT

Amazonia 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 life forms provides unique genetic resources, adaptations, and ecological functions that contribute to ecosystem services globally. The Amazon 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 include: (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, and when 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 Western Amazonia, and contributed to the origin of the modern transcontinental Amazon river, (iv) 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, 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 and fully document the genetic and ecological resources of the singular Amazonian biota. 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.

GRAPHICAL ABSTRACT


Transformations of Amazonian landscapes through the Cenozoic Era

Evolutionary and ecological processes influencing local and regional biodiversity


The current Amazon basin and the main biogeographic regions of the Neotropics

Graphical Abstract. The evolution of Amazonian diversity. (A) Transformations of Amazonian landscapes through the Cenozoic Era. Brown = uplands (> ca. 300 m elevation). Yellow = lowlands. Greens = tropical forests. Blue = mega-wetlands. Blue arrows = main river drainages. Dates in presented millions of years ago (Ma). **(B)** Evolutionary and ecological processes influencing local and regional biodiversity. Species are added to the Amazonian species pool by the processes of speciation and dispersal, removed by the process of extinction, and modified by the processes of natural selection and genetic drift. **(C)** The current Amazon basin and the main biogeographic regions of the Neotropics.

1. DELIMITATION OF AMAZONIA

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 1).**

Figure 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.

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**). Amazonian diversity also represents a bewildering range of life forms, ecological functions, chemical compounds, and genetic resources (Darst *et al.* 2006; Asner *et al.* 2014; Albert *et al.* 2020a, **Figure 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 results from the extremely high number of species found in the region (Magurran and McGill 2011; Raven *et al.* 2020), the numerous species with subtle phenotypic differences (Angulo and Icochea 2010; Benzaquem *et al.* 2015; Draper *et al.* 2020), the logistic difficulties associated 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 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).

A 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 the non-linear interactions among Amazonian species and their **abiotic** environments. For example, while it is clear that the Amazon 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 the Amazonian **biota**, especially the more recent speciation events (Rull 2011). Until recently, a fragmentary knowledge of Amazonian biodiversity at finer **taxonomic** levels has 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 financial resources to maintain and expand their collections (Fontaine *et al.* 2012; Funk 2018). Human 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.

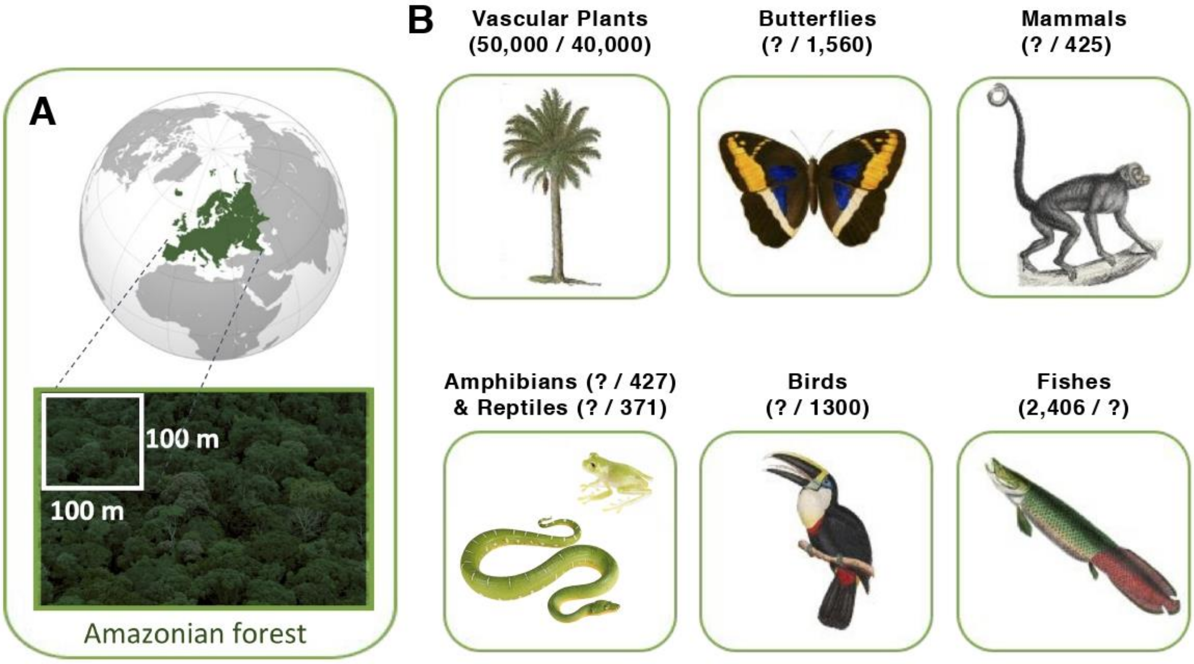


Figure 2. The Amazon biota in numbers. **A.** More species of flowering plants are found in a 10,000 m^2 area of Amazon Rainforest than in the whole of Europe (Ter Steege *et al.* 2006). **B.** Estimated numbers of species of selected Amazonian lineages for the Amazon basin, followed by numbers for the Amazon Rainforest, 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).

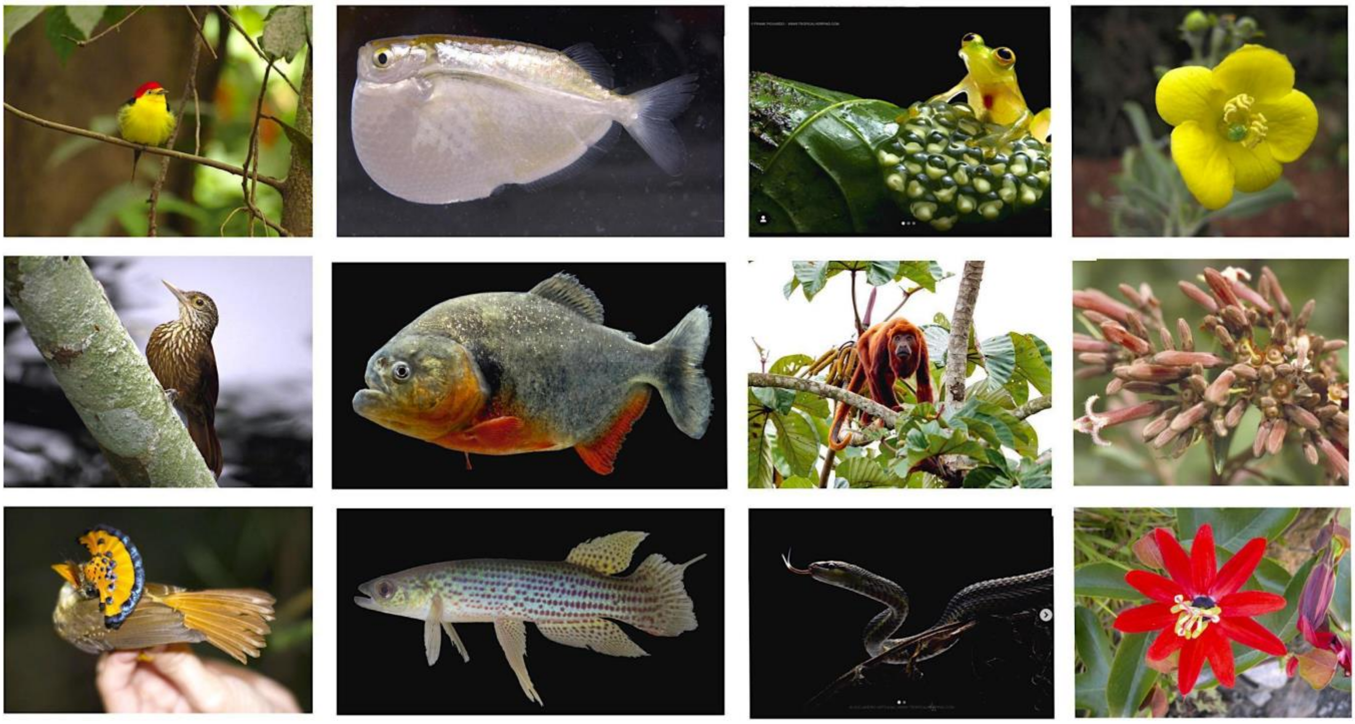


Figure 3. A small sample of Amazonian biodiversity. **First column:** Wire-tailed manakin (*Pipra filicauda*), Amazonian Royal Flycatcher (*Onychorhynchus coronatus*). **Second column:** Amazon Flying Fish (*Thoracocharax stellatus*), Red Bellied Piranha (*Pygocentrus cariba),* Redspot Killifish (*Trigonectes 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 (first column), James Albert (second column), Tropical Herping (third column), and Carmen Ulloa Ulloa (fourth column).

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 the Neotropical ecosystems did not become dominated by flowering plants 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 Amazonia 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 along this period (Antonelli *et al.* 2009).

Amazonia was substantially modified by the sudden mass extinction triggered by the impact of a large bolide (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 after that. Plant communities similar to those seen in the Neotropical rainforests today, 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 into two - the Amazon and Atlantic rainforests - due to the 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, as well as that of the Northern Andes, both of which contributed to substantial changes in South American air currents (see Chapter 1). The 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, an uplift of the Northern Andes led to a profound reorganization of the river network and the formation of the **Pebas** mega wetland system (Hoorn *et al.* 1995, 2010, 2017; Albert *et al.* 2018), with the establishment of vast lacustrine and swampy environments in western Amazonia (Hoorn 1993; Wesselingh and Salo 2006). The 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 western Amazonia 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 the overfilling of the western Amazonian sedimentary basins with Andean-derived sediments. This led to a renewed drainage reorganization and the onset of the modern transcontinental Amazon River (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). In the Late Miocene (ca. 11 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 (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 the 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, together with geomorphological processes, strongly altered the western Amazonian landscape. **Alluvial megafans** (large sediment aprons >10,000 sq. km) extended from the Andes into Amazonia (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 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 the 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 affect the distribution of specialized species (Arruda *et al.* 2017; Wang *et al.* 2017; Silva *et al.* 2019).

Current data fail to support the Pleistocene Refugia hypothesis as originally proposed by Haffer (1969), one of the better known hypotheses for Amazonian diversification. The Refugia hypothesis proposed that Pleistocene climatic oscillations led to the cyclic replacement of forested 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 Amazonia (Liu and Colinvaux 1985; Colinvaux *et al.* 2000; Bush and Oliveira 2006), although several upland regions of Eastern Amazonia have experienced substantial changes in vegetation structure (Cowling *et al.* 2001; Arruda *et al.* 2017). 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), fishes (Lundberg *et al.* 2009), and even some mammals (Defler *et al.* 2019). 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).

4. ASSEMBLING THE MEGADIVERSE AMAZONIAN BIOTA

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 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. Generally, 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 lineages older than those of the lowland river basins located near the geographic core of the continent. This pattern is observed in many taxonomic groups (e.g. plants, Ulloa and Neill 2006; Amazonian rocket frogs *Allobates,* see **Figure 6**, Réjaud *et al.* 2020; fishes, Albert *et al.* 2020a), although exceptions also exist (e.g. in some frog groups, 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). Although all regional biotas are composed of taxa with a broad range of evolutionary ages, the age profile is skewed to older ages on the shields relative to the lowlands. While both young and old species are found in the shields and base of the Andes, species assemblages in the sedimentary basins are mostly composed of younger species.

Diversification in response to geographic barriers is one of the most widespread processes that facilitates speciation. In Amazonia, 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 5, 6, 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.

Changes in river drainage networks have also strongly affected dispersal, gene flow, and biotic diversification within Amazonia (**Figure 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 the 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 for species diversification in this region. For example, the large geographical extension of Amazonia, tied to its diverse soil types, have provided multiple opportunities for ecological specialization (BOX 1; Fine *et al.* 2005; Tuomisto *et al.* 2019). This soil heterogeneity observed in Amazonia reflects the complex geological history of northern South America (see Chapter 1, section 4.1). While the erosion of the Guiana and Brazilian shields produced the soils of east Amazonia, the younger sediments that are products of the Andean Orogeny have developed soils in western Amazonia 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 the annual flooding cycle have contributed to the formation 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 5.1).

****

BOX 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 Amazonia (white-sand, clay, and terrace soils). 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 the 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, indicating that the adaptations necessary to occupy these open vegetation habitats may not be common within forest specialized groups.

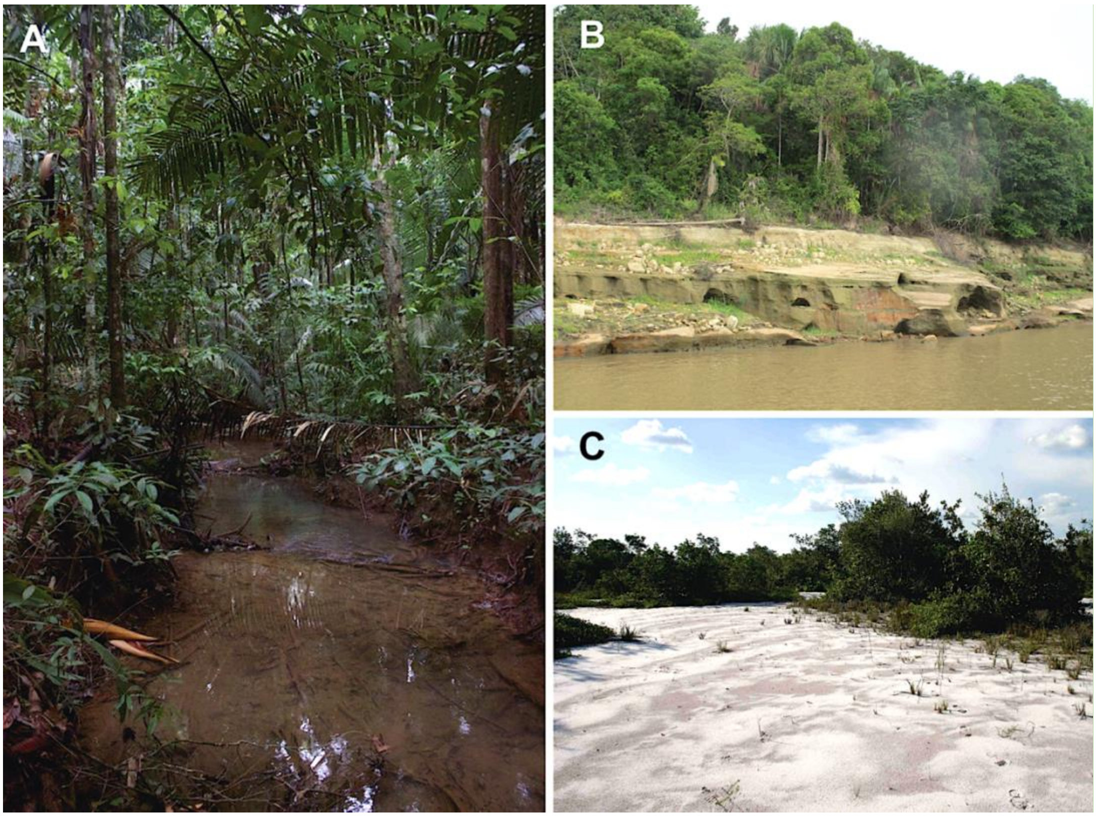


Figure caption (Box 1). Plants and bird species adapt to habitats with different soils. (A) Clay-soil forest. (B) Terrace-soil forest. (C) White-sand vegetation. Photos by Camila Ribas.

****

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. The 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 4000 m, exhibit an immense gradient of humidity and temperature. This has provided numerous opportunities of 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," significantly increasing the 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).

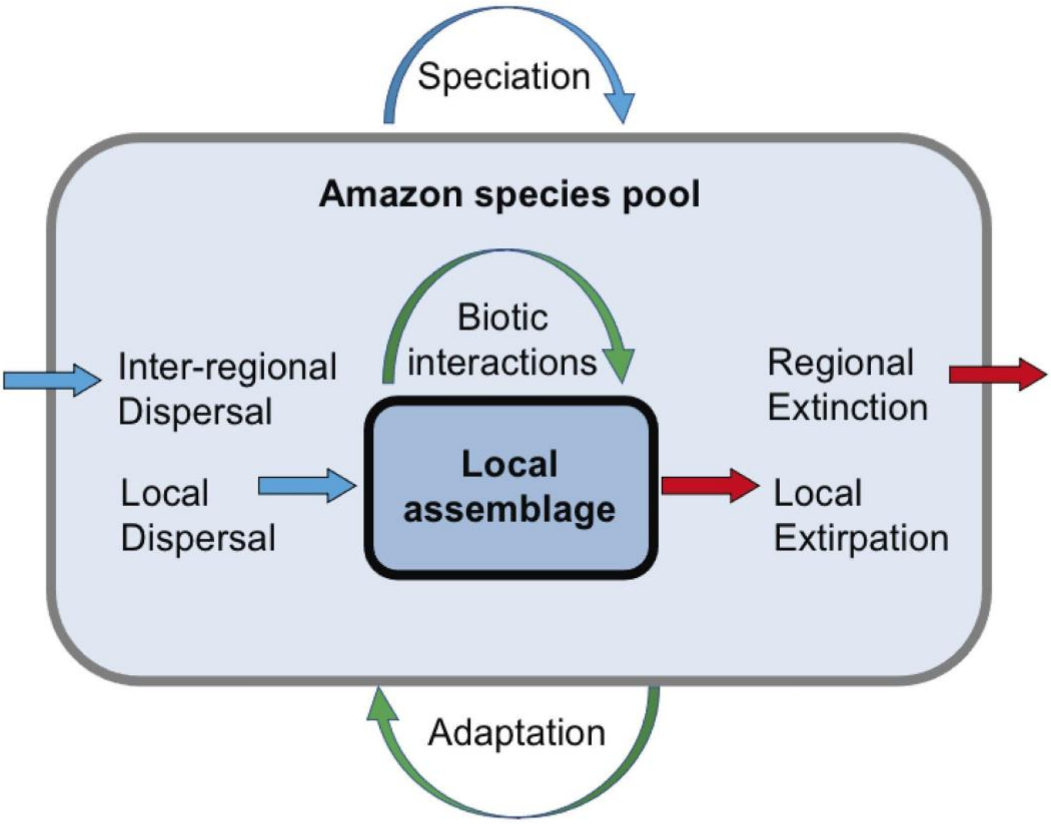


Figure 4. Regional and local processes underlying the assembly of the Amazonian biota. The regional species pool (outer light-blue box) is defined as the sum of all the local species assemblages (inner dark-blue box). Blue arrows indicate processes that increase species richness, red arrows highlight 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).

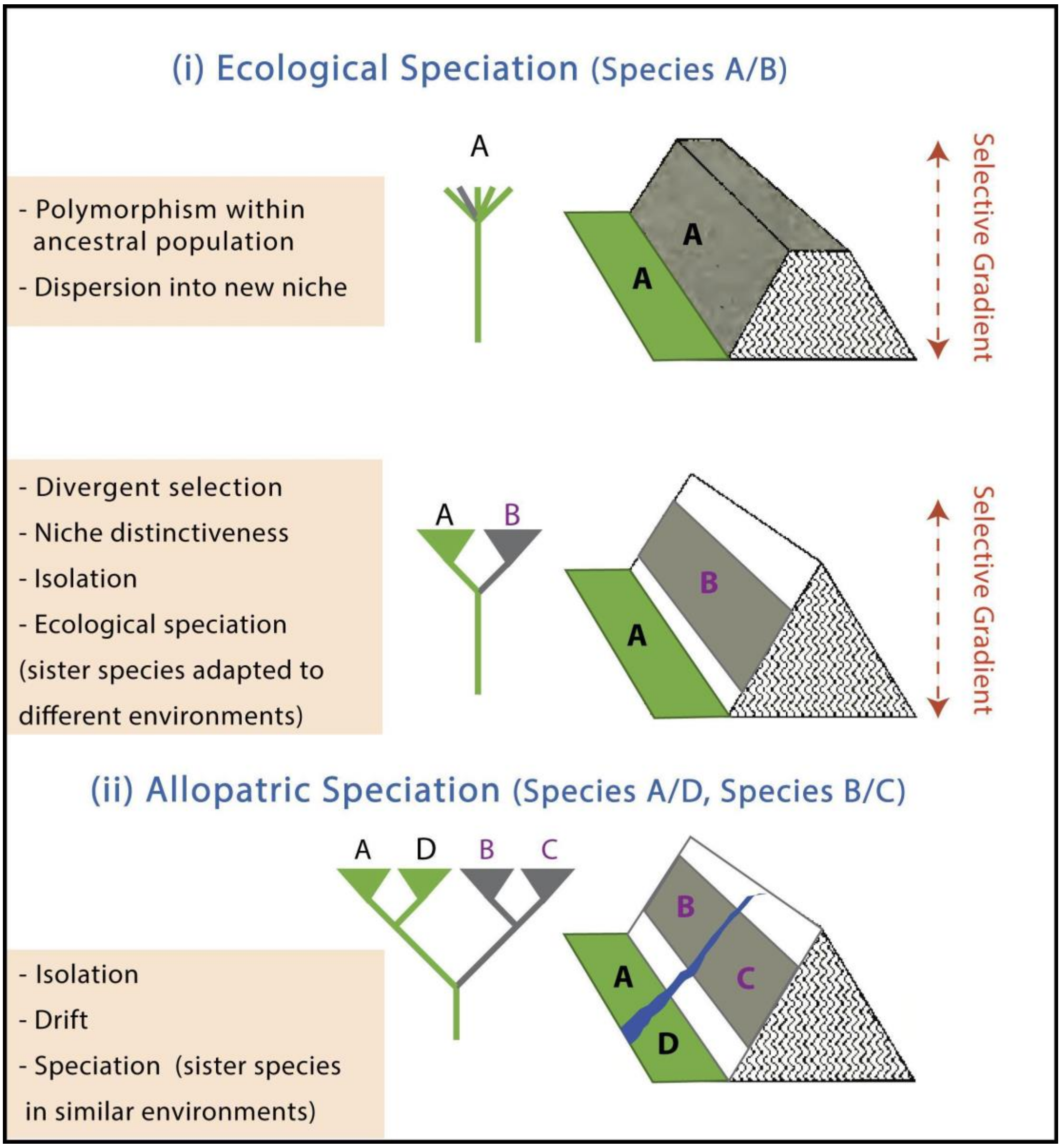


Figure 5. Common speciation mechanisms in Amazonia and elsewhere. (i) *Ecological speciation* is the process by which new species form as a consequence of selection along climatic or ecological gradients, such as those encountered in the Andes. Note that the resulting species occupy distinct environments. (ii) *Allopatric speciation* occurs 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).

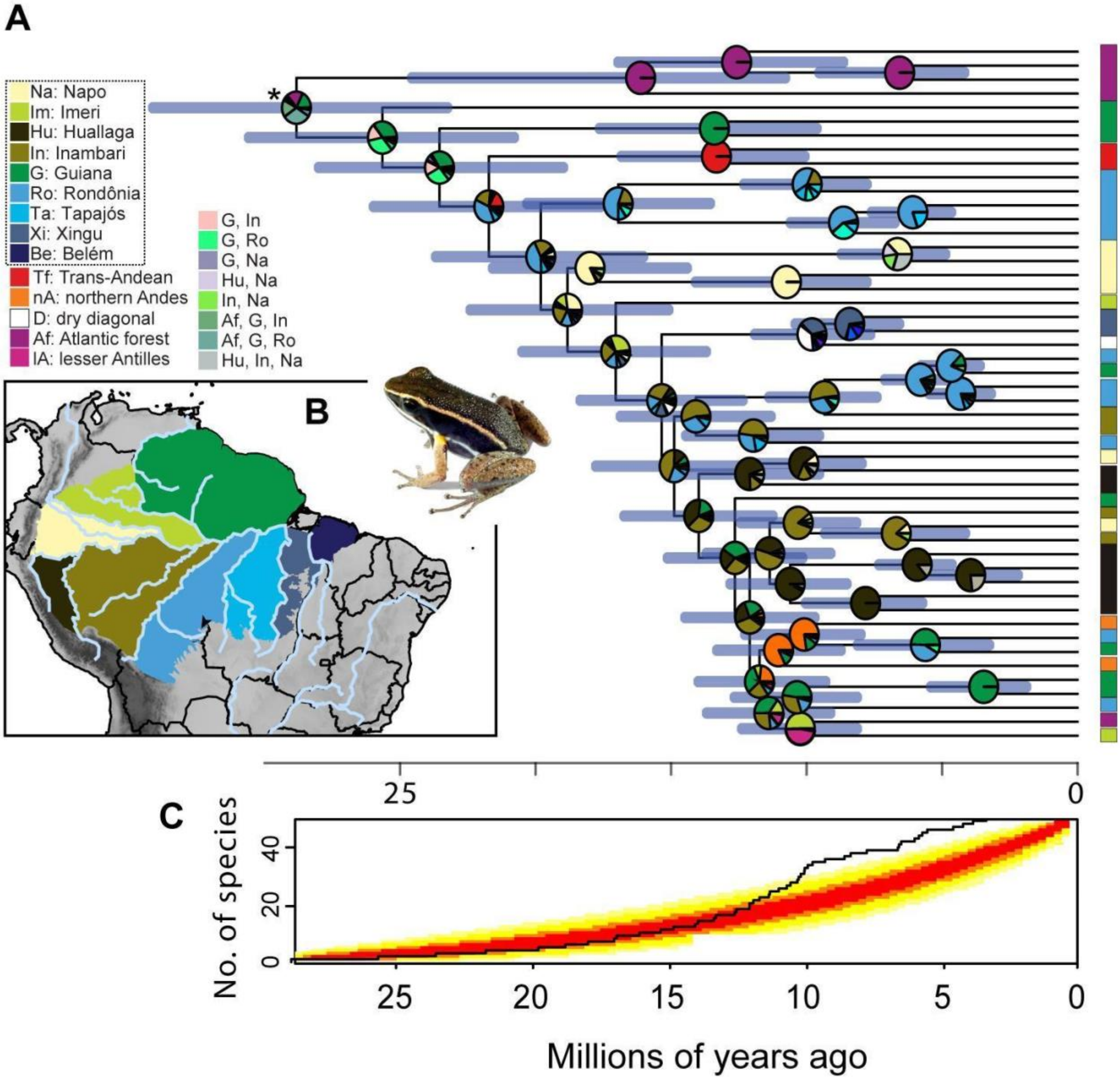


Figure 6. Diversification and endemism in the Amazonian rocket frogs (*Allobates* spp). Closely related species display an allopatric pattern of distribution, matching interfluves delimited by modern Amazonian rivers. **(A)** Evolutionary relationships, represented as a phylogenetic tree. Time is provided 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, coloured 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 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 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 Amazonia results from both abiotic (see **4.2. Geographical connectivity through time**) and biotic (see 4.4.**. How biodiversity generates and maintains biodiversity**) factors.

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 demographic and genetic connections in some groups can reduce connections in others. For example, while large lowland rivers such as the Amazonas 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 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 Amazonia 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 an 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 abilities, for example, facilitate geographic isolation and genetic differentiation that 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 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 promote speciation. Lowland tropical species also live under temperature conditions close to their thermal maximum, which places them at risk in the face of increased 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 the 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, 2019b, 2021), and even some small-bodied fishes (Dagosta and Pinna 2017), serving as an effective barrier for some species but not for others. Species traits and their ecology are hence important not only to define their current distributions and degree of connectivity, 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. Again, changes in precipitation patterns may affect forest adapted populations differently, depending on their association with humid microhabitats. 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). The resilience of the upland forest taxa has relied historically on the large dimensions of suitable habitat that allowed movements 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). Understanding these historical dynamics lays 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.

4.3. Trait mediated diversification in a heterogeneous Amazonia

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 Amazonia. 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 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 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 the Amazonian floodplains (Bicudo *et al.* 2019). Data from floodplain-adapted birds and fishes, for instance, indicate historically larger and more connected populations in Western Amazonia (Santos *et al.* 2007; Thom *et al.* 2020), and cycles of connectivity and isolation between species that occupy seasonally flooded habitats in Eastern vs. Western Amazonia. 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 Amazonia. 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 the open vegetation of sandy soils has been heterogeneously distributed for millions of years (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 of these distributions as they occur at the present time.

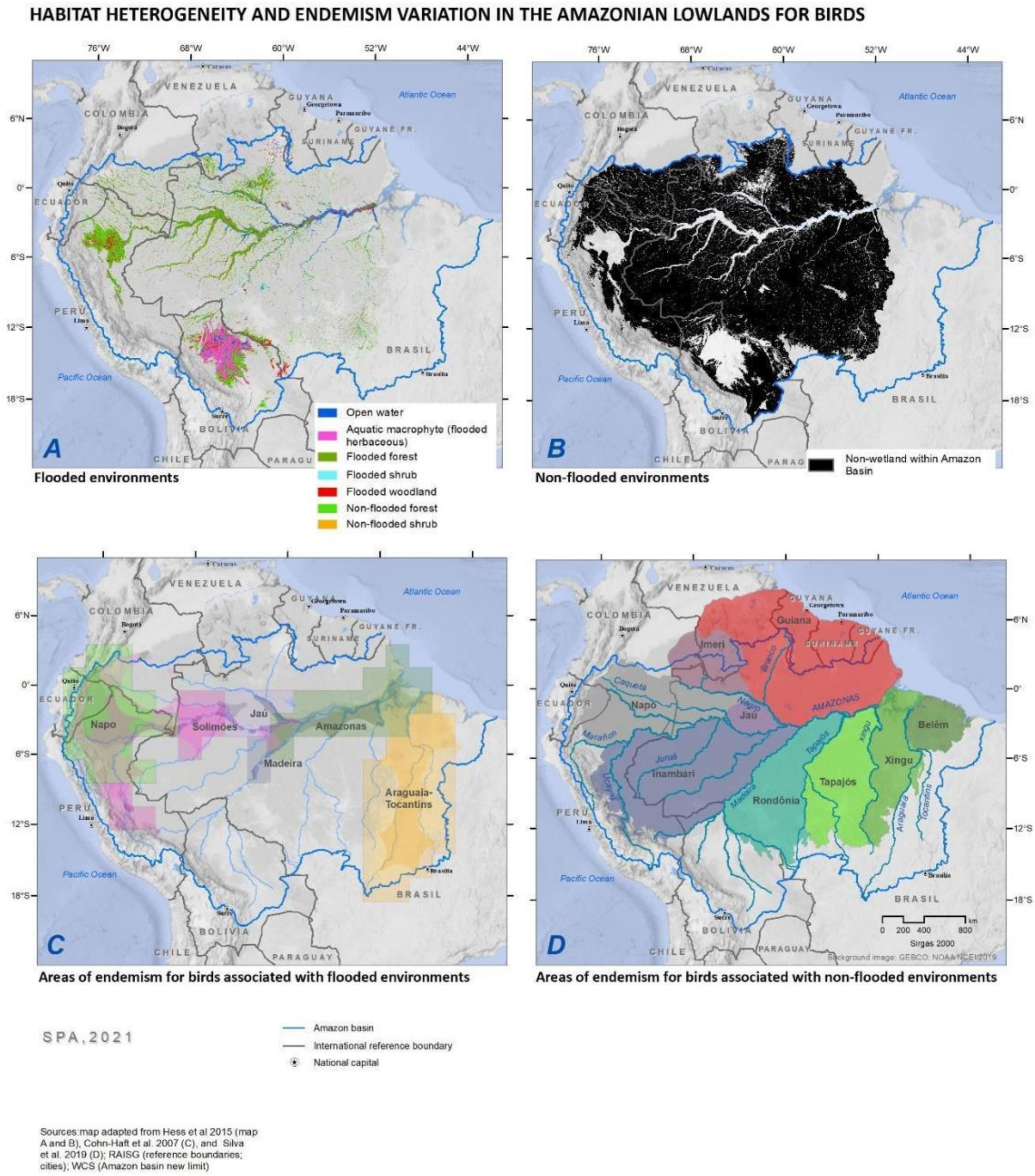


Figure 7: Habitat heterogeneity and bird distribution and endemism in the Amazonian floodplains. Distribution of (A) flooded (~14% of the total area) and (B) non-flooded environments (modified from Hess *et al.* 2015). Areas of endemism for birds associated with (C) flooded (Cohn-Halt *et al*., 2007) and (D) non-flooded (Silva *et al.* 2019) environments.

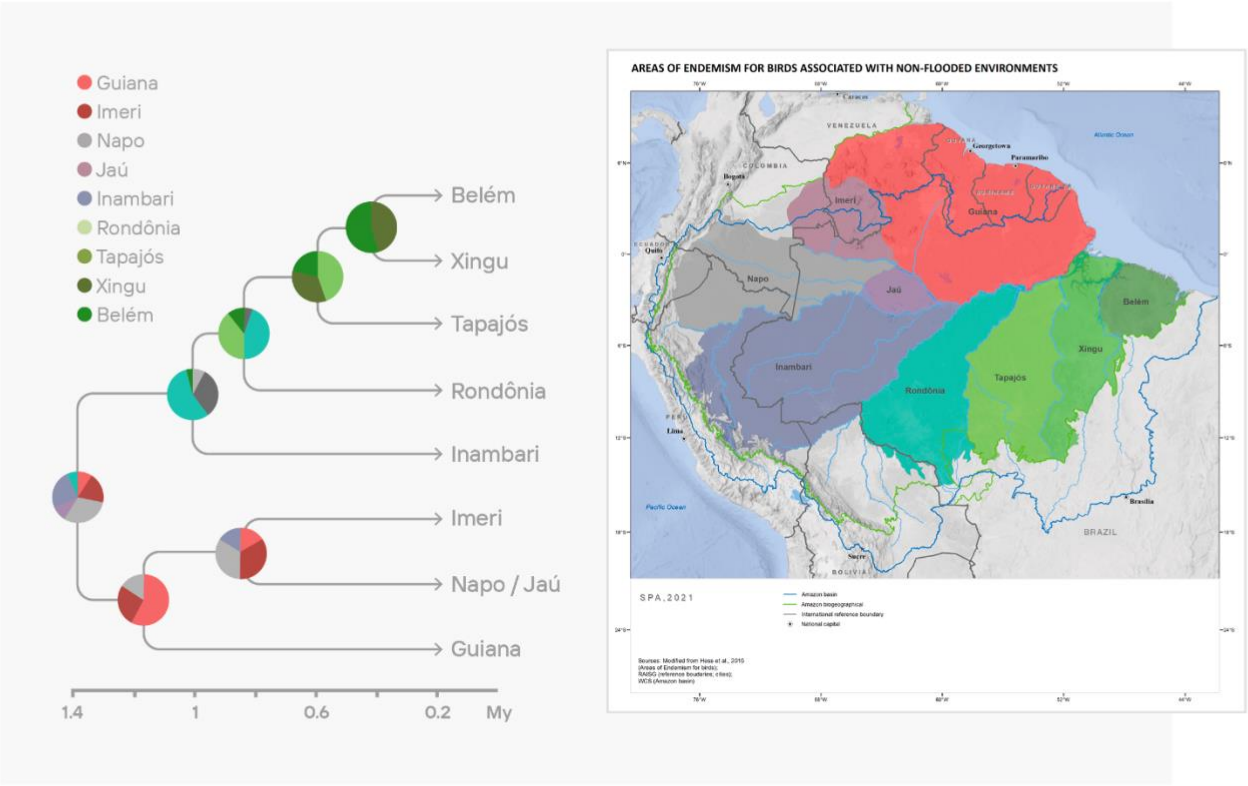


Figure 8. Summary of diversification patterns for 21 taxonomic clades of Amazonian birds restricted to the upland forest (terra firme) understory. ***Left:*** Relationships among nine areas of endemism, inferred from genetic data; pie charts denote ancestral area probabilities. ***Right:*** Areas of 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. 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/Jau) from those south of it (Inambari, Rondonia, Tapajós, Belém, Xingu). Modified from Silva *et al*. (2019).

4.4. How biodiversity generates and maintains biodiversity

There is little doubt that diverse biotas with many functionally distinct kinds of organisms, complex biotic environments, and multiple ecological interactions and opportunities facilitate species coexistence and elevate regional species richness and species density values. In this regard, biological diversity may be understood to be **autocatalytic:** species richness itself is a key feature in the origin of the 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, the 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. Because 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). 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 defences from the arthropod prey that they feed upon. These **alkaloids** (**BOX 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, reflecting 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 goes 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).

****

BOX 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 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 a 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).

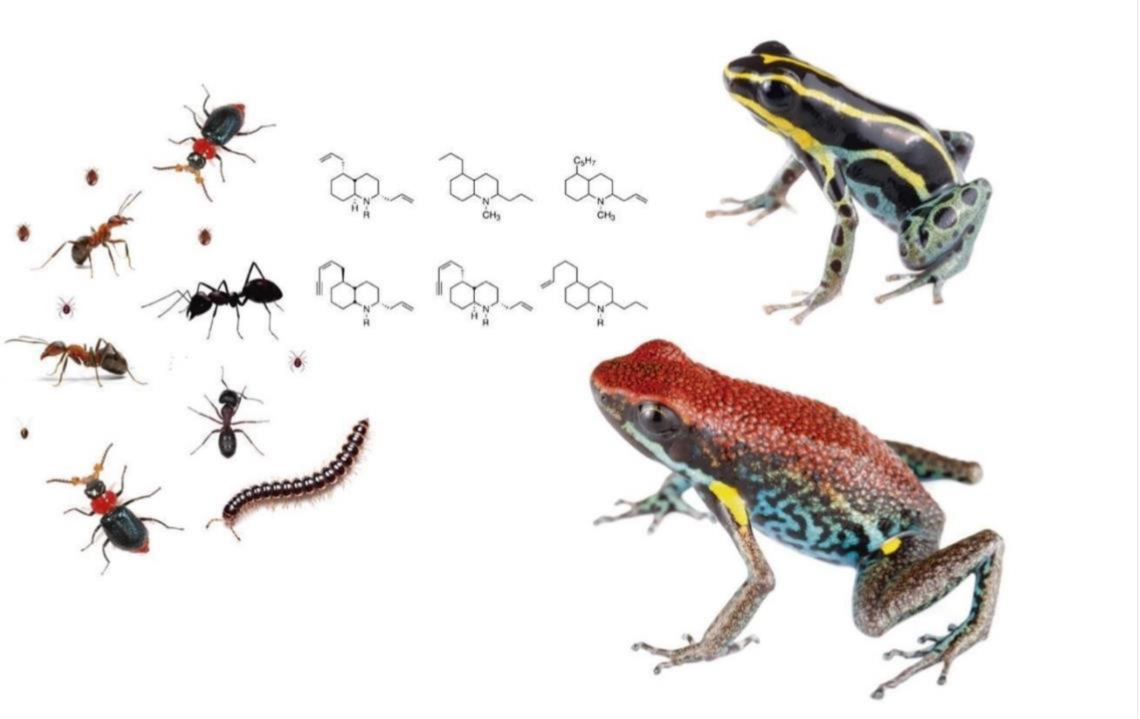


Figure caption (Box 2). Poison dart frogs are protected by alkaloids that they sequester from their prey, including ants, mites, millipedes, and melyrid beetles.

****

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 extinctions 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.

Throughout its lengthy geological history, the Pan-Amazonian region has undergone extensive environmental changes, driven primarily by regional tectonic and global climatic forces. Pan-Amazonia 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) 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). These events resulted in the establishment of a sub-Andean river basin draining north towards a large embayment of the

Caribbean Sea that extended over the area that is now occupied by the Colombian and Venezuelan Llanos.

(ii) Mountain building in the Central and Northern Andes. This narrowed the Caribbean influence and led to the origin and movement of mega-wetlands in Western Amazonia ca. 22–10 Ma. The Pebas mega-wetland system resulted from that expansion reaching a maximum area of more than 1 million km^2 (see Chapter 1).

(iii) An intense Andean mountain building since the late-middle Miocene (last 10 Ma), coinciding with global fluctuations in sea level. This prevented further marine influences into Western Amazonia and along the northern Andean foreland basin, retaining much of the drainages that flowed into the Pacific and the Caribbean and forming the wide floodplain named Acre System.

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

(v) The full closing of the Panama Isthmus (ca. 3.5 Ma). This provided opportunities for extensive migrations of North American lineages to both Amazonia and the 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 3**). While the geological record does not provide evidence of sudden mass extinction events during the Cenozoic history of Amazonia, 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. Pulses of extinctions between each of those stages are attested by the fossil record. The most significant extinctions were those affecting the rich and endemic lacustrine fauna, notably of bivalve molluscs (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).

Molluscs and crocodylians are among the best represented clades in the fossil record of Amazonia. They exemplify the diversification and subsequent extinction of the 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 molluscs colonized the Western Amazon during pulses 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 crocodylians evolved crushing dentitions that allowed them to feed on hard-shelled organisms and prey on the Pebasian malacofauna (Salas-Gismondi *et al*. 2015). The crocodylian 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 Amazonia 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.

With the end of the Pebas System, most of the associated molluscan fauna became extinct. Consequently, the modern Amazonian mollusc diversity is remarkably poor and dominated by cosmopolitan freshwater groups, such as freshwater mussels, clams, and snails (Wesselingh and Ramos 2010). As an outcome of the vanishment of the Pebasian endemic molluscs, the Pan-Amazonian crocodylians suffered its first important extinction event (Salas-Gismondi *et al.* 2015, Souza-Filho *et al*. 2019).

Most of the crocodylian lineages survived to the establishment of the following Acre System, ca. 10–7 millions 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 crocodylian fauna, extant or extinct (Riff *et al.* 2010; Cidade *et al.* 2019). Similarly, there was a high diversity of turtles, including one of the largest turtles that ever lived on Earth, with more than 2.5 m in length and estimated body mass of ca. 1,000 kg (Cadena *et al.* 2020b). Beyond some of the generalist genera that exist until our days (e.g. *Caiman*, *Melanosuchus*, and *Paleosuchus*), which have been present in the Amazon since the Middle Miocene, the availability of large-bodied prey and the competition with other aquatic predators likely triggered the evolution of giant top predators. Examples include *Purussaurus brasiliensis*, with its 12-meter long 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 over the crocodylian fauna. All specialized forms, from small to giant, vanished. The extant South American crocodylians are now a small fraction of their former diversity. Entire body types and ecological roles among the aquatic fauna disappeared after the demise of the Amazonian Miocene mega-wetlands.

In stark contrast to the high turnover of molluscs and crocodylians, the modern Amazonia fish fauna remains largely unchanged at the genus level and higher. Direct evidence from the fossil record indicates that all but one fossil genus known from the Miocene of tropical South America 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 the South America to harbour a peculiar and endemic mammalian megafauna, 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 the 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; 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 Amazonia, and most of the Neotropical placental mammals, such as felids, canids, peccaries, deers, otters, tree squirrels, camelids, as well the extincts proboscidians and horses, are descendents of North Americans migrants (Webb 1991; Antonelli *et al.* 2018).

A global-scale extinction of the megafauna impacted Amazonia at the end of the Pleistocene. It reduced the 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 at least ~26% to 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 the megafauna extinction (Doughty *et al.* 2016b).

The global fossil record shows us that species with specialized diets, large body sizes, broad distributions, longer life spans, slow reproduction, and few offsprings 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 crocodylians 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 current environmental pressures currently faced by Amazonia such as hunting, 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 threat (Shahabuddin and Ponte 2005).

****

BOX 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 caption (Box 3). 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 & Wesselingh (2010).

****

6. HUMANS HAVE INFLUENCED THE AMAZON BASIN FOR THOUSANDS OF YEARS

Humans may have occupied the Americas much earlier than previously thought. New records date back to 33,000–31,000 years ago in Mexico (Ardelean *et al.* 2020) and 13,000 years ago in the tropical Americas (Roosevelt et al. 2013). As such, human impact on local ecosystems, including those in Amazonia, 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, influencing current patterns of Amazonian biodiversity (Heckenberger and Neves 2009; Shepard and Ramirez 2011).

Although the 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 for 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 Amazonia, 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 fishery 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), for instance, 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).

7. 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 Amazonia is lacking in all the major biodiversity dimensions, including taxonomic diversity, geographic distributions, species abundances, phylogenetic relationships , species traits , and species interactions.

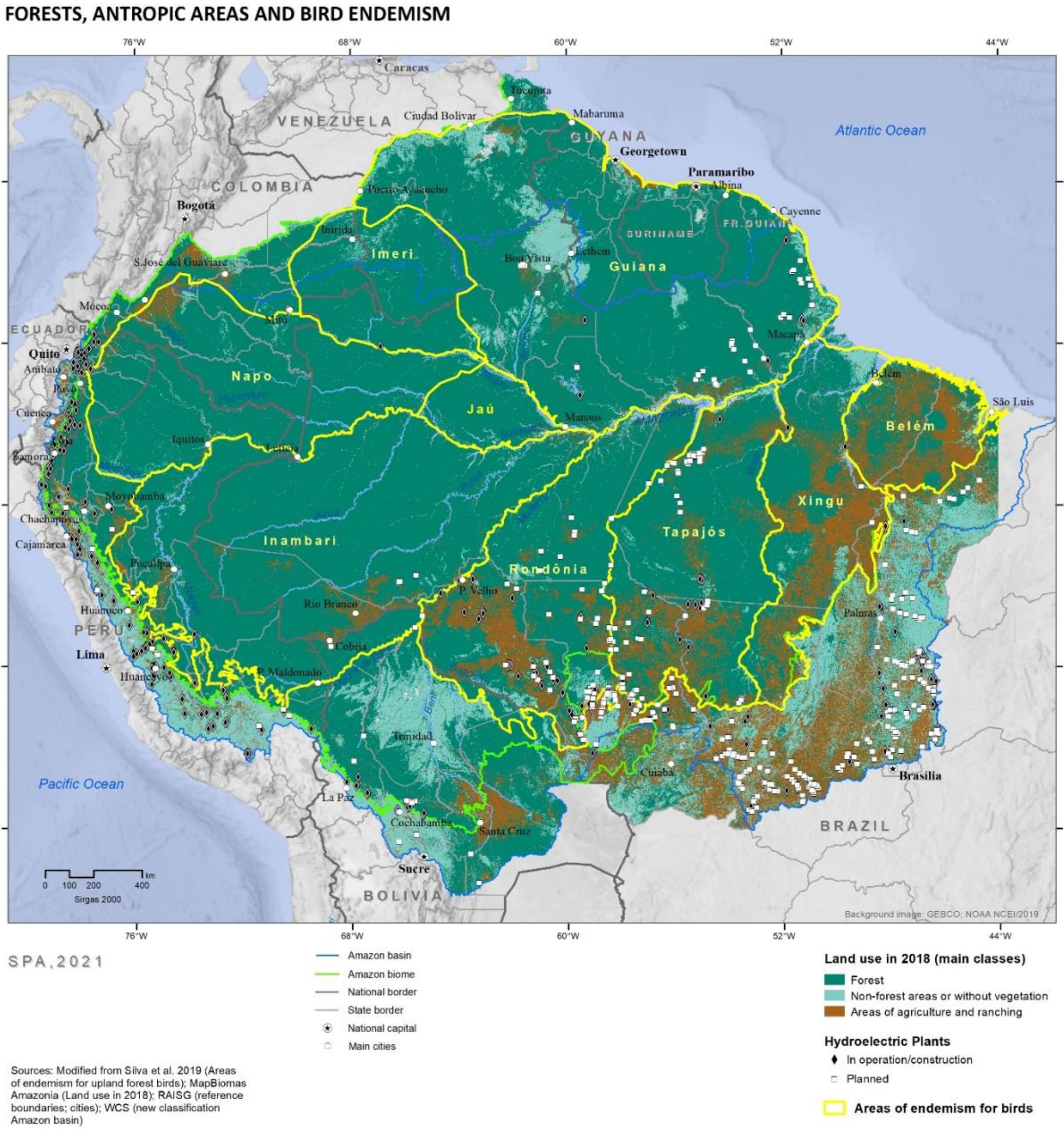
The main threats to Amazonian diversity, just like its ecosystems and landscapes, are heterogeneously distributed (RAISG, 2020; **Figure 9**). As such, a one-fits-all strategy will not work in the region. Effective conservation strategies must consider the evolutionary and ecological processes that generate 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 Amazonia (and globally) is based primarily on individual species. Both governmental initiatives (e.g. Endangered Species Act) and non-governmental policies (e.g. IUCN Red Lists) 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 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 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 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 5)**, is relevant from an evolutionary standpoint. In Amazonia, for instance, adjacent yet distinct soil types are intimately associated with plant specialization and differentiation (Fine *et al.* 2005). Promoting conservation of these 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 Amazonia 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 into biodiversity and ecosystem function in all other South and Central American regions. Current declines in Amazonian biodiversity (WWF 2016) threaten the evolutionary process governing the origin and maintenance of species diversity in all of these areas. 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 Amazonia 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 taken into account in regional planning and during rainforest conservation efforts. The establishment of river impoundments, for instance, interrupt natural flood regimes and disrupt the 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).



Sources: Modified from Silva et al. 2019 (Areas of endemism for upland forest birds); MapBiomas Amazonia (Land use in 2018); RAISG (reference boundaries; cities); WCS (new classification Amazon basin)

Figure 9. Deforested (red), forested (green), dams (black diamonds), and avian areas of endemism (yellow polygons) in Amazonia. Note the greatest immediate threats to Amazonian biodiversity are located along the agricultural frontier in southeastern Amazonia, especially impacting the southeastern areas of endemism. Note the large number of dams in the Andes and on the Brazilian Shield.

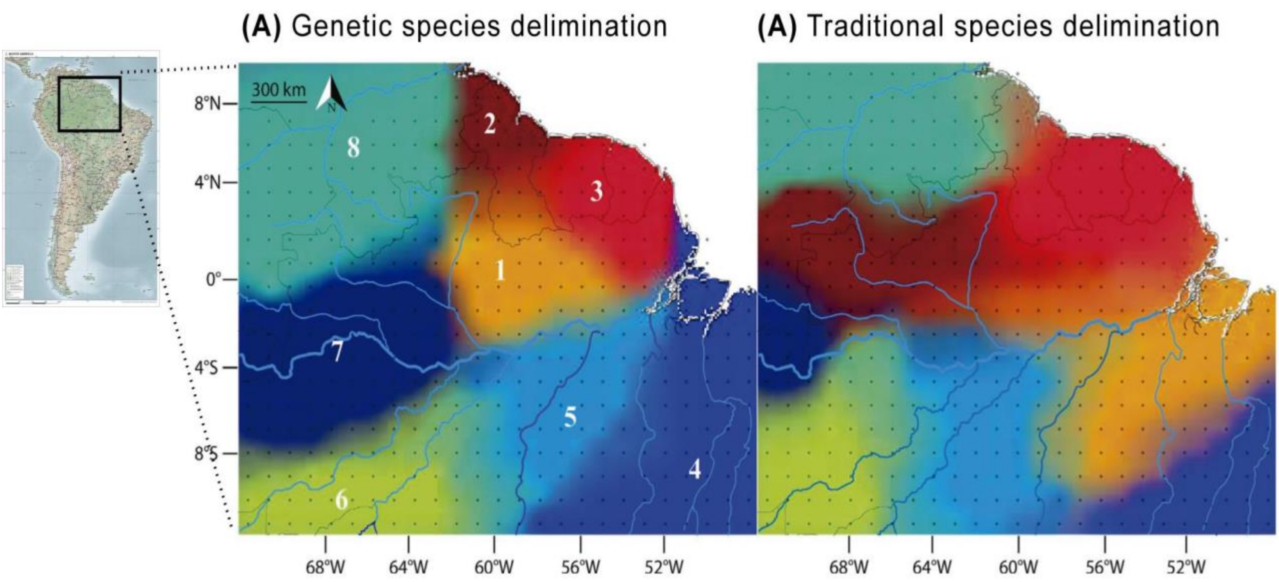


Figure 10. Bioregionalization based on species occurrence data for frogs in the Eastern Amazon. **A**. Data from DNA-based species delimitation. **B**. Data from morphology-based taxonomy. Colors represent affiliations of cells to bioregions. Note both the bioregion boundaries and numbers of endemic species are sensitive to which dataset is used. Images modified from Vacher et al. (2020).

8. 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 the Amazonian ecosystems accelerated with Portuguese and Spanish colonization in the past 500 years, 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 agricultural and cattle production and other human activities (e.g. logging, mining, hunting, fishing, dams, roads) are profoundly affecting the species richness and evolutionary processes of the Amazon basin 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).

9. 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.

Main 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 trainining 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 genetic and environmental characterization of cryptic and poorly known species, including especially soil and aquatic fungi and microbes.

Main 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.
- Give specific attention to ecological and evolutionary processes and their conservation, recognizing that they will differ across Amazonian environments and ecosystems.
- Establish and maintain long-term partnerships with local Indigenous and non-Indigenous communities, to exchange critical biodiversity information between academic and local knowledge bases.
- Prioritize conservation action in areas where anthropogenic threats are maximized (e.g., endemicity areas in southeastern Brazil; **Figure 9**).
- Develop ecosystem-level plans for infrastructure, especially water impoundments (e.g. dams) and roads.

10. REFERENCES

Adeney JM, Christensen NL, Vicentini A, and Cohn-Haft M. 2016. White-sand Ecosystems in Amazonia. *Biotropica* **48**: 7–23.

Albert JS, Carvalho TP, Petry P, *et al.* 2011b. Aquatic biodiversity in the Amazon: habitat specialization and geographic isolation promote species richness. *Animals* **1**: 205–41.

Albert JS, Destouni G, Duke-Sylvester SM, *et al.* 2020b. Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio* **50**: 85–94.

Albert JS, Lovejoy NR, and Crampton WGR. 2006. Miocene tectonism and the separation of cis- and trans-Andean river basins: Evidence from Neotropical fishes. *J South Am Earth Sci* **21**: 14–27.

Albert JS, Petry P, and Reis RE. 2011a. Major Biogeographic and Phylogenetic Patterns. In: Historical Biogeography of Neotropical Freshwater Fishes. University of California Press.

Albert JS, Tagliacollo VA, and Dagosta F. 2020a. Diversification of Neotropical Freshwater Fishes. *Annu Rev Ecol Evol Syst* **51**: 27–53.

Albert JS, Val P, and Hoorn C. 2018. The changing course of the Amazon River in the Neogene: center stage for Neotropical diversification. *Neotrop Ichthyol* **16**.

Alda F, Tagliacollo VA, Bernt MJ, *et al.* 2019. Resolving deep nodes in an ancient radiation of neotropical fishes in the presence of conflicting signals from incomplete lineage sorting. *Syst Biol* **68**: 573–93.

Anderson EP, Jenkins CN, Heilpern S, *et al.* 2018. Fragmentation of Andes-to-Amazon connectivity by hydropower dams. *Sci Adv* **4**: eaao1642.

Angulo A and Icochea J. 2010. Cryptic species complexes, widespread species and conservation: lessons from Amazonian frogs of the Leptodactylus marmoratus group (Anura: Leptodactylidae). *Syst Biodivers* **8**: 357–70.

Antoine P-O, Abello MA, Adnet S, *et al.* 2016. A 60-million-year Cenozoic history of western Amazonian ecosystems in Contamana, eastern Peru. *Gondwana Res* **31**: 30–59.

Antonelli A, Nylander JAA, Persson C, and Sanmart\'\in I. 2009. Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proc Natl Acad Sci* **106**: 9749–54.

Antonelli A, Zizka A, Carvalho FA, *et al.* 2018. Amazonia is the primary source of Neotropical biodiversity. *Proc Natl Acad Sci* **115**: 6034–9.

Ardelean CF, Becerra-Valdivia L, Pedersen MW, *et al.* 2020. Evidence of human occupation in Mexico around the Last Glacial Maximum. *Nature* **584**: 87–92.

Arruda DM, Schaefer CEGR, Fonseca RS, *et al.* 2017. Vegetation cover of Brazil in the last 21 ka: new insights into the Amazonian refugia and Pleistocenic arc hypotheses. *Glob Ecol Biogeogr* **27**: 47–56.

Asner GP, Martin RE, Tupayachi R, *et al.* 2014. Amazonian functional diversity from forest canopy chemical assembly. *Proc Natl Acad Sci* **111**: 5604–9.

Aureliano T, Ghilardi AM, Guilherme E, *et al.* 2015. Morphometry, bite-force, and paleobiology of the Late Miocene Caiman Purussaurus brasiliensis. *PLoS One* **10**: e0117944.

Ayres JM and Clutton-Brock TH. 1992. River boundaries and species range size in Amazonian primates. *Am Nat* **140**: 531–7.

Azevedo JAR, Guedes TB, Nogueira C de C, *et al.* 2020. Museums and cradles of diversity are geographically coincident for narrowly distributed Neotropical snakes. *Ecography (Cop)* **43**: 328–39.

Bacon CD, Silvestro D, Jaramillo C, *et al.* 2015. Biological evidence supports an early and complex emergence of the Isthmus of Panama. *Proc Natl Acad Sci* **112**: 6110–5.

Bacon CD, Velásquez-Puentes FJ, Hoorn C, and Antonelli A. 2018. Iriarteeae palms tracked the uplift of Andean Cordilleras. *J Biogeogr* **45**: 1653–63.

Bambach RK. 2006. Phanerozoic biodiversity mass extinctions. *Annu Rev Earth Planet Sci* **34**: 127–55.

Barnosky AD and Lindsey EL. 2010. Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. *Quat Int* **217**: 10–29.

Barnosky AD, Koch PL, Feranec RS, *et al.* 2004. Assessing the causes of late Pleistocene extinctions on the continents. *Science* **306**: 70–5.

Barnosky AD. 2004. Assessing the Causes of Late Pleistocene Extinctions on the Continents. *Science* **306**: 70–5.

Barrowclough GF, Cracraft J, Klicka J, and Zink RM. 2016. How many kinds of birds are there and why does it matter? *PLoS One* **11**: e0166307.

Barthem RB, Goulding M, Leite RG, *et al.* 2017. Goliath catfish spawning in the far western Amazon confirmed by the distribution of mature adults, drifting larvae and migrating juveniles. *Sci Rep* **7**: 1–13.

Bass MS, Finer M, Jenkins CN, *et al.* 2010. Global conservation significance of Ecuador's Yasun{\'\i} National Park. *PLoS One* **5**: e8767.

Bates JM and Demos TC. 2001. Do we need to devalue Amazonia and other large tropical forests? *Divers Distrib* **7**: 249–55.

Benchimol M and Peres CA. 2015. Predicting local extinctions of Amazonian vertebrates in forest islands created by a mega dam. *Biol Conserv* **187**: 61–72.

Benítez-López A, Santini L, Schipper AM, *et al.* 2019. Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. *PLoS Biol* **17**: e3000247.

Benton MJ. 2009. The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. *Science* **323**: 728–32.

Benzaquem DC, Oliveira C, Silva Batista J da, *et al.* 2015. DNA barcoding in pencilfishes (Lebiasinidae: Nannostomus) reveals cryptic diversity across the Brazilian Amazon. *PLoS One* **10**: e0112217.

Bicudo TC, Sacek V, Almeida RP de, *et al.* 2019. Andean tectonics and Mantle Dynamics as a Pervasive Influence on Amazonian ecosystem. *Sci Rep* **9**: 1–11.

Bigarella JJ. 1975. Considerações a respeito das mudanças paleoambientais na distribuição de algumas espécies vegetais e animais no Brasil. *An Acad Bras Cienc* **47**: 411–64.

Billerman SM, Keeney BK, Rodewald PG, and Schulenberg TS. 2020. Birds of the World. *Ithaca, New York Cornell Lab Ornithol*.

Blisniuk PM, Stern LA, Chamberlain CP, *et al.* 2005. Climatic and ecologic changes during Miocene surface uplift in the Southern Patagonian Andes. *Earth Planet Sci Lett* **230**: 125–42.

Bodmer RE, Eisenberg JF, and Redford KH. 1997. Hunting and the likelihood of extinction of Amazonian mammals: Caza y Probabilidad de Extinción de Mamiferos Amazónicos. *Conserv Biol* **11**: 460–6.

Bonaccorso E and Guayasamin JM. 2013. On the origin of Pantepui montane biotas: a perspective based on the phylogeny of Aulacorhynchus toucanets. *PLoS One* **8**: e67321.

Boonstra M, Ramos MIF, Lammertsma EI, *et al.* 2015. Marine connections of Amazonia: Evidence from foraminifera and dinoflagellate cysts (early to middle Miocene, Colombia/Peru). *Palaeogeogr Palaeoclimatol Palaeoecol* **417**: 176–94.

Boubli JP, Ribas C, Lynch Alfaro JW, *et al.* 2015. Spatial and temporal patterns of diversification on the Amazon: A test of the riverine hypothesis for all diurnal primates of Rio Negro and Rio Branco in Brazil. *Mol Phylogenet Evol* **82**: 400–12.

Bouchenak-Khelladi Y, Slingsby JA, Verboom GA, and Bond WJ. 2014. Diversification of C4 grasses (Poaceae) does not coincide with their ecological dominance. *Am J Bot* **101**: 300–7.

Brooks DR, Mayden RL, and McLennan DA. 1992. Phylogeny and biodiversity: Conserving our evolutionary legacy. *Trends Ecol Evol* **7**: 55–9.

Brodie ED Jr and Tumbarello MS. 1978. The antipredator functions of Dendrobates auratus (Amphibia, Anura, Dendrobatidae) skin secretion in regard to a snake predator (Thamnophis). J Herpetol 12: 264–265.

Brower AVZ. 1996. Parallel race formation and the evolution of mimicry in Heliconius butterflies: a phylogenetic hypothesis from mitochondrial DNA sequences. *Evolution (N Y)* **50**: 195–221.

Brown D. 2009. Biogeography. Sinauer Associates.

Burnham RJ and Graham A. 1999. The history of neotropical vegetation: new developments and status. *Ann Missouri Bot Gard*: 546–89.

Burnham RJ and Johnson KR. 2004. South American palaeobotany and the origins of neotropical rainforests. *Philos Trans R Soc London Ser B Biol Sci* **359**: 1595–610.

Bush MB and Oliveira PE de. 2006. The rise and fall of the Refugial Hypothesis of Amazonian speciation: a paleoecological perspective. *Biota Neotrop* **6**: 0.

Byrne H, Rylands AB, Carneiro JC, *et al.* 2016. Phylogenetic relationships of the New World titi monkeys (Callicebus): first appraisal of taxonomy based on molecular evidence. *Front Zool* **13**: 1–26.

Cadena CD, Cuervo AM, Céspedes LN, *et al.* 2020a. Systematics, biogeography, and diversification of Scytalopus tapaculos (Rhinocryptidae), an enigmatic radiation of Neotropical montane birds. *Auk* **137**: ukz077.

Cadena E-A, Scheyer TM, Carrillo-Briceño JD, *et al.* 2020b. The anatomy, paleobiology, and evolutionary relationships of the largest extinct side-necked turtle. *Sci Adv* **6**: eaay4593.

Campos DF, Val AL, and Almeida-Val VMF. 2018. The influence of lifestyle and swimming behavior on metabolic rate and thermal tolerance of twelve Amazon forest stream fish species. *J Therm Biol* **72**: 148–54.

Canal D, Köster N, Celis M, *et al.* 2019. Out of Amazonia and Back again: Historical Biogeography of the Species-Rich Neotropical Genus Philodendron (Araceae) 1. *Ann Missouri Bot Gard* **104**: 49–68.

Capurucho JMG, Borges SH, Cornelius C, *et al.* 2020. Patterns and processes of diversification in Amazonian white sand ecosystems: insights from birds and plants. In: Neotropical diversification: patterns and processes. Springer.

Cardoso D, Särkinen T, Alexander S, *et al.* 2017. Amazon plant diversity revealed by a taxonomically verified species list. *Proc Natl Acad Sci* **114**: 10695–700.

Carrillo JD, Forasiepi A, Jaramillo C, and SÃ¡nchez-Villagra MR. 2015. Neotropical mammal diversity and the Great American Biotic Interchange: spatial and temporal variation in South America’s fossil record. *Front Genet* **5**: 451.

Carvalho Francisco JN and Lohmann LG. 2020. Phylogeny and Biogeography of the Amazonian Pachyptera (Bignonieae, Bignoniaceae). *Syst Bot* **45**: 361–74.

Carvalho MR, Herrera FA, Jaramillo CA, *et al.* 2011. Paleocene Malvaceae from northern South America and their biogeographical implications. *Am J Bot* **98**: 1337–55.

Carvalho MR, Jaramillo C, la Parra F de, *et al.* 2021. Extinction at the end-Cretaceous and the origin of modern Neotropical rainforests. *Science* **372**: 63–8.

Castelnau F comte de. 1855. Animaux nouveaux ou rares recueillis pendant l’expedition dans les parties centrales de L’Amerique du Sud, de Rio de Janeiro a Lima, et de Lima au Para. Tome Second. FR: Chez P. Bertrand.

Castro RB, Pereira JLG, Albernaz ALKM, and Zanin M. 2020. Connectivity, spatial structure and the identification of priority areas for conservation of Belém area of endemism, Amazon. *An Acad Bras Cienc* **92**.

Castroviejo-Fisher S, Guayasamin JM, Gonzalez-Voyer A, and Vilà C. 2014. Neotropical diversification seen through glassfrogs. *J Biogeogr* **41**: 66–80.

Ceballos G, Ehrlich PR, Barnosky AD, *et al.* 2015. Accelerated modern human--induced species losses: Entering the sixth mass extinction. *Sci Adv* **1**: e1400253.

Chambers JQ, Asner GP, Morton DC, *et al.* 2007. Regional ecosystem structure and function: ecological insights from remote sensing of tropical forests. *Trends Ecol \& Evol* **22**: 414–23.

Cheng H, Sinha A, Cruz FW, *et al.* 2013. Climate change patterns in Amazonia and biodiversity. *Nat Commun* **4**: 1411.

Chichorro F, Juslén A, and Cardoso P. 2019. A review of the relation between species traits and extinction risk. *Biol Conserv* **237**: 220–9.

Cidade GM, Fortier D, and Hsiou AS. 2019. The crocodylomorph fauna of the Cenozoic of South America and its evolutionary history: a review. *J South Am Earth Sci* **90**: 392–411.

Claramunt S and Cracraft J. 2015. A new time tree reveals Earth history's imprint on the evolution of modern birds. *Sci Adv* **1**: e1501005.

Cody S, Richardson JE, Rull V, *et al.* 2010. The great American biotic interchange revisited. *Ecography (Cop)* **33**: 326–32.

Colinvaux PA, Oliveira PE De, and Bush MB. 2000. Amazonian and neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. *Quat Sci Rev* **19**: 141–69.

Colwell RK, Brehm G, Cardelús CL, *et al.* 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* **322**: 258–61.

Cooper N, Bielby J, Thomas GH, and Purvis A. 2008. Macroecology and extinction risk correlates of frogs. *Glob Ecol Biogeogr* **17**: 211–21.

Cordell GA, Quinn-Beattie M Lou, and Farnsworth NR. 2001. The potential of alkaloids in drug discovery. *Phyther Res An Int J Devoted to Pharmacol Toxicol Eval Nat Prod Deriv* **15**: 183–205.

Costa GC, Hampe A, Ledru M-P, *et al.* 2017. Biome stability in South America over the last 30 kyr: Inferences from long-term vegetation dynamics and habitat modelling. *Glob Ecol Biogeogr* **27**: 285–97.

Costa LP. 2003. The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. *J Biogeogr* **30**: 71–86.

Cowling SA, Maslin MA, and Sykes MT. 2001. Paleovegetation simulations of lowland Amazonia and implications for neotropical allopatry and speciation. *Quat Res* **55**: 140–9.

Coyne JA and Orr HA. Speciation. Sinauer Associates, Inc.

Cracraft J, Ribas CC, d'Horta FM, *et al.* 2020. The origin and evolution of Amazonian species diversity. In: Neotropical diversification: patterns and processes. Springer.

Cracraft J. 1985. Historical Biogeography and Patterns of Differentiation within the South American Avifauna: Areas of Endemism. *Ornithol Monogr*: 49–84.

Craig JM, Crampton WGR, and Albert JS. 2017. Revision of the polytypic electric fish Gymnotus carapo (Gymnotiformes, Teleostei), with descriptions of seven subspecies. *Zootaxa* **4318**: 401–38.

Croft DA. 2016. Horned armadillos and rafting monkeys: the fascinating fossil mammals of South America. Indiana University Press.

Dagosta FCP and Pinna M de. 2017. Biogeography of Amazonian fishes: deconstructing river basins as biogeographic units . *Neotrop Ichthyol* **15**.

Daly JW, Secunda SI, Garraffo HM, et al. 1992. Variability in alkaloid profiles in neotropical poison frogs (Dendrobatidae): genetic versus environmental determinants. Toxicon 30: 887–898.

Daly JW, Garraffo HM, Spande TF, *et al.* 2003. Evidence for an enantioselective pumiliotoxin 7-hydroxylase in dendrobatid poison frogs of the genus Dendrobates. *Proc Natl Acad Sci* **100**: 11092–7.

Daly JW, Martin Garraffo H, Spande TF, *et al.* 2000. Alkaloids from frog skin: the discovery of epibatidine and the potential for developing novel non-opioid analgesics. *Nat Prod Rep* **17**: 131–5.

Daly JW, Ware N, Saporito RA, *et al.* 2009. N-methyldecahydroquinolines: an unexpected class of alkaloids from Amazonian poison frogs (Dendrobatidae). *J Nat Prod* **72**: 1110–4.

Damasco G, Daly DC, Vicentini A, and Fine PVA. 2019. Reestablishment of Protium cordatum (Burseraceae) based on integrative taxonomy. *Taxon* **68**: 34–46.

Dambros C, Zuquim G, Moulatlet GM, *et al.* 2020. The role of environmental filtering, geographic distance and dispersal barriers in shaping the turnover of plant and animal species in Amazonia. *Biodivers Conserv* **29**: 3609–34.

Darst CR, Cummings ME, and Cannatella DC. 2006. A mechanism for diversity in warning signals: conspicuousness versus toxicity in poison frogs. *Proc Natl Acad Sci* **103**: 5852–7.

Dáttilo W and Dyer L. 2014. Canopy Openness Enhances Diversity of Ant–Plant Interactions in the Brazilian Amazon Rain Forest. *Biotropica* **46**: 712–9.

Defler T. 2019. History of Terrestrial Mammals in South America. Cham: Springer International Publishing.

Diele-Viegas LM, Vitt LJ, Sinervo B, *et al.* 2018. Thermal physiology of amazonian lizards (reptilia: Squamata). *PLoS One* **13**: e0192834.

Diele-Viegas LM, Werneck FP, and Rocha CFD. 2019. Climate change effects on population dynamics of three species of Amazonian lizards. *Comp Biochem Physiol Part A Mol \& Integr Physiol* **236**: 110530.

Dino R, Pocknall DT, and Dettmann ME. 1999. Morphology and ultrastructure of elater-bearing pollen from the Albian to Cenomanian of Brazil and Ecuador: implications for botanical affinity. *Rev Palaeobot Palynol* **105**: 201–35.

Dobson A, Lafferty KD, Kuris AM, *et al.* 2008. Homage to Linnaeus: how many parasites? How many hosts? *Proc Natl Acad Sci* **105**: 11482–9.

Doughty CE, Roman J, Faurby S, *et al.* 2016. Global nutrient transport in a world of giants. *Proc Natl Acad Sci* **113**: 868–73.

Doughty CE, Wolf A, Morueta-Holme N, *et al.* 2016. Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests. *Ecography (Cop)* **39**: 194–203.

Draper FC, Baker TR, Baraloto C, *et al.* 2020. Quantifying Tropical Plant Diversity Requires an Integrated Technological Approach. *Trends Ecol \& Evol.*

Duellman WE. 1999. Patterns of distribution of amphibians: a global perspective. JHU Press.

Duran-Bautista EH, Armbrecht I, Acioli ANS, *et al.* 2020. Termites as indicators of soil ecosystem services in transformed amazon landscapes. *Ecol Indic* **117**: 106550.

Edwards EJ and Smith SA. 2010. Phylogenetic analyses reveal the shady history of C4 grasses. *Proc Natl Acad Sci* **107**: 2532–7.

Edwards EJ, Osborne CP, Strömberg CAE, *et al.* 2010. The origins of C4 grasslands: integrating evolutionary and ecosystem science. *Science* **328**: 587–91.

Erkens RHJ, Chatrou LW, Maas JW, *et al.* 2007. A rapid diversification of rainforest trees (Guatteria; Annonaceae) following dispersal from Central into South America. *Mol Phylogenet Evol* **44**: 399–411.

Erwin TL. 1991. An Evolutionary Basis for Conservation Strategies. *Science* **253**: 750–2.

Escobar H. 2019. Amazon fires clearly linked to deforestation, scientists say. *Science* **365**: 853 LP – 853.

Espeland M, Breinholt J, Willmott KR, *et al.* 2018. A Comprehensive and Dated Phylogenomic Analysis of Butterflies. *Curr Biol* **28**: 770-778.e5.

Espeland M, Hall JPW, DeVries PJ, *et al.* 2015. Ancient Neotropical origin and recent recolonisation: Phylogeny, biogeography and diversification of the Riodinidae (Lepidoptera: Papilionoidea). *Mol Phylogenet Evol* **93**: 296–306.

Fecchio A, Pinheiro R, Felix G, *et al.* 2018. Host community similarity and geography shape the diversity and distribution of haemosporidian parasites in Amazonian birds. *Ecography (Cop)* **41**: 505–15.

Fernandes CC, Podos J, and Lundberg JG. 2004. Amazonian ecology: tributaries enhance the diversity of electric fishes. *Science* **305**: 1960–2.

Fine PA, Daly DC, and Cameron KM. 2005. The contribution of edaphic heterogeneiyt to the evolution and diversity of burseracear trees in the western Amazon. *Evolution (N Y)* **59**: 1464–78.

Flanagan NS, Ospina-Calderón NH, Agapito LTG, *et al.* 2018. A new species of Vanilla (Orchidaceae) from the North West Amazon in Colombia. *Phytotaxa* **364**: 250–8.

Flecker AS. 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. *Ecology* **77**: 1845–54.

Folgarait PJ. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodivers \& Conserv* **7**: 1221–44.

Fontaine B, Achterberg K van, Alonso-Zarazaga MA, *et al.* 2012. New Species in the Old World: Europe as a Frontier in Biodiversity Exploration, a Test Bed for 21st Century Taxonomy (B Schierwater, Ed). *PLoS One* **7**: e36881.

Forest F, Grenyer R, Rouget M, *et al.* 2007. Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* **445**: 757–60.

Fouquet A, Recoder R, Teixeira Jr M, *et al.* 2012. Molecular phylogeny and morphometric analyses reveal deep divergence between Amazonia and Atlantic Forest species of Dendrophryniscus. *Mol Phylogenet Evol* **62**: 826–38.

Friedman M. 2010. Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. *Proc R Soc B Biol Sci* **277**: 1675–83.

Fritz G, Rand AS, and dePamphilis CW. 1981. The aposematically colored frog, Dendrobates pumilio, is distasteful to the large predatory ant, Paraponera clavata. Biotropica 13: 158–159.

Funk VA. 2018. Collections-based science in the 21st century. *J Syst Evol* **56**: 175–93.

García-Melo JE, Oliveira C, Costa Silva GJ Da, *et al.* 2019. Species delimitation of neotropical Characins (Stevardiinae): Implications for taxonomy of complex groups (Z Peng, Ed). *PLoS One* **14**: e0216786.

García-Robledo C, Kuprewicz EK, Baer CS, *et al.* 2020. The Erwin equation of biodiversity: From little steps to quantum leaps in the discovery of tropical insect diversity. *Biotropica* **52**: 590–7.

Gauld ID, Gaston KJ, and Janzen DH. 1992. Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the" nasty" host hypothesis. *Oikos*: 353–7.

Gehara M, Crawford AJ, Orrico VGD, *et al.* 2014. High levels of diversity uncovered in a widespread nominal taxon: continental phylogeography of the Neotropical tree frog Dendropsophus minutus. *PLoS One* **9**: e103958.

Gentry AH. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Ann Missouri Bot Gard* **69**: 557–93.

Ghai R, Rod\'r\'\iguez-Valera F, McMahon KD, *et al.* 2011. Metagenomics of the water column in the pristine upper course of the Amazon river. *PLoS One* **6**: e23785.

Givnish TJ, Spalink D, Ames M, *et al.* 2016. Orchid historical biogeography, diversification, Antarctica and the paradox of orchid dispersal. *J Biogeogr* **43**: 1905–16.

Godinho MB de C and Silva FR da. 2018. The influence of riverine barriers, climate, and topography on the biogeographic regionalization of Amazonian anurans. *Sci Rep* **8**: 3427.

Gould J, Gould E, Hart WM, *et al.* 1852. A monograph of the Ramphastidae, or family of toucans. London : Published by the author, 20, Broad Street, Golden Square,.

Goulding M, Venticinque E, Ribeiro ML de B, *et al.* 2019. Ecosystem-based management of Amazon fisheries and wetlands. *Fish Fish* **20**: 138–58.

Gross M. 2019. Finding the cradles of evolution. *Curr Biol* **29**: R71–3.

Guayasamin JM, Cisneros-Heredia DF, McDiarmid RW, *et al.* 2020. Glassfrogs of Ecuador: diversity, evolution, and conservation. *Diversity* **12**: 222.

Haffer J. 1969. Speciation in Amazonian Forest Birds. *Science* **165**: 131–7.

Häggi C, Chiessi CM, Merkel U, *et al.* 2017. Response of the Amazon rainforest to late Pleistocene climate variability. *Earth Planet Sci Lett* **479**: 50–9.

Head JJ, Bloch JI, Hastings AK, *et al.* 2009. Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature* **457**: 715–7.

Heckenberger M and Neves EG. 2009. Amazonian archaeology. *Annu Rev Anthropol* **38**: 251–66.

Heckenberger M. 2005. The ecology of power: culture, place, and personhood in the southern Amazon, AD 1000-2000. Psychology Press.

Hess LL, Melack JM, Affonso AG, *et al.* 2015. Wetlands of the lowland Amazon basin: Extent, vegetative cover, and dual-season inundated area as mapped with JERS-1 synthetic aperture radar. *Wetlands* **35**: 745–56.

Hewitson WC, Saunders WW, and Schaus W. 1856. Illustrations of new species of exotic butterflies : selected chiefly from the collections of W. Wilson Saunders and William C. Hewitson / by William C. Hewitson. London : John Van Voorst,.

Hoorn C, Bogotá-A GR, Romero-Baez M, *et al.* 2017. The Amazon at sea: Onset and stages of the Amazon River from a marine record, with special reference to Neogene plant turnover in the drainage basin. *Glob Planet Change* **153**: 51–65.

Hoorn C, Guerrero J, Sarmiento GA, and Lorente MA. 1995. Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. *Geology* **23**: 237–40.

Hoorn C, Ham R van der, la Parra F de, *et al.* 2019. Going north and south: The biogeographic history of two Malvaceae in the wake of Neogene Andean uplift and connectivity between the Americas. *Rev Palaeobot Palynol* **264**: 90–109.

Hoorn C, Wesselingh FP, Steege H ter, *et al.* 2010. Amazonia Through Time: Andean Uplift, Climate Change, Landscape Evolution, and Biodiversity. *Science* **330**: 927–31.

Hoorn C. 1993. Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: results of a palynostratigraphic study. *Palaeogeogr Palaeoclimatol Palaeoecol* **105**: 267–309.

Hoorn C. 1994. An environmental reconstruction of the palaeo-Amazon river system (Middle--Late Miocene, NW Amazonia). *Palaeogeogr Palaeoclimatol Palaeoecol* **112**: 187–238.

Hopkins MJG. 2007. Modelling the known and unknown plant biodiversity of the Amazon Basin. *J Biogeogr* **34**: 1400–11.

Hubbell SP, He F, Condit R, *et al.* 2008. How many tree species are there in the Amazon and how many of them will go extinct? *Proc Natl Acad Sci* **105**: 11498 LP – 11504.

Hughes LC, Ortí G, Huang Y, *et al.* 2018. Comprehensive phylogeny of ray-finned fishes (Actinopterygii) based on transcriptomic and genomic data. *Proc Natl Acad Sci* **115**: 6249–54.

Hutter CR, Guayasamin JM, and Wiens JJ. 2013. Explaining Andean megadiversity: the evolutionary and ecological causes of glassfrog elevational richness patterns. *Ecol Lett* **16**: 1135–44.

Jacobs BF and Currano ED. 2021. The impactful origin of neotropical rainforests. *Science* **372**: 28 LP – 29.

Janzen DH. 1967. Why mountain passes are higher in the tropics. *Am Nat* **101**: 233–49.

Jaramillo AF, La Riva I De, Guayasamin JM, *et al.* 2020. Vastly underestimated species richness of Amazonian salamanders (Plethodontidae: Bolitoglossa) and implications about plethodontid diversification. *Mol Phylogenet Evol* **149**: 106841.

Jaramillo C, Hoorn C, Silva SAF, *et al.* 2010a. The origin of the modern Amazon rainforest: implications of the palynological and palaeobotanical record. *Amaz Landsc species Evol* **317**: 334.

Jaramillo C, Ochoa D, Contreras L, *et al.* 2010b. Effects of rapid global warming at the Paleocene-Eocene boundary on neotropical vegetation. *Science* **330**: 957–61.

Jaramillo C, Romero I, D'Apolito C, *et al.* 2017. Miocene flooding events of western Amazonia. *Sci Adv* **3**: e1601693.

Jaramillo C, Rueda MJ, and Mora G. 2006. Cenozoic plant diversity in the Neotropics. *Science* **311**: 1893–6.

Jardine W and Courier P-L. 1840. Monkeys. London : Chatto & Windus,.

Jenkins CN, Pimm SL, and Joppa LN. 2013. Global patterns of terrestrial vertebrate diversity and conservation. *Proc Natl Acad Sci* **110**: E2602--E2610.

Jetz W, Thomas GH, Joy JB, *et al.* 2012. The global diversity of birds in space and time. *Nature* **491**: 444–8.

Jézéquel C, Tedesco PA, Darwall W, *et al.* 2020. Freshwater fish diversity hotspots for conservation priorities in the Amazon Basin. *Conserv Biol* **34**: 956–65.

Jost L. 2004. Explosive local radiation of the genus Teagueia (Orchidaceae) in the Upper Pastaza watershed of Ecuador. *Lyonia* **7**: 41–7.

Kay R, Madden R, Cifelli RL, and Flynn J. 1997. Vertebrate paleontology in the Neotropics. The Miocene fauna of La Venta. DC, USA: Smithsonian Institution Press.

Kirschner JA and Hoorn C. 2020. The onset of grasses in the Amazon drainage basin, evidence from the fossil record. *Front Biogeogr* **12**.

Kistler L, Yoshi Maezumi S, Souza JG De, *et al.* 2018. Multiproxy evidence highlights a complex evolutionary legacy of maize in South America. *Science* **362**: 1309–13.

Lagomarsino LP, Condamine FL, Antonelli A, *et al.* 2016. The abiotic and biotic drivers of rapid diversification in A ndean bellflowers (Campanulaceae). *New Phytol* **210**: 1430–42.

LaPolla JS, Dlussky GM, and Perrichot V. 2013. Ants and the Fossil Record. *Annu Rev Entomol* **58**: 609–30.

Latrubesse EM, Arima EY, Dunne T, *et al.* 2017. Damming the rivers of the Amazon basin. *Nature* **546**: 363–9.

Levis C, Costa FRC, Bongers F, *et al.* 2017. Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science* **355**: 925–31.

Liu K and Colinvaux PA. 1985. Forest changes in the Amazon Basin during the last glacial maximum. *Nature* **318**: 556–7.

Lohmann LG, Bell CD, Calió MF, and Winkworth RC. 2013. Pattern and timing of biogeographical history in the Neotropical tribe Bignonieae (Bignoniaceae). *Bot J Linn Soc* **171**: 154–70.

Loiselle BA, Jørgensen PM, Consiglio T, *et al.* 2008. Predicting species distributions from herbarium collections: does climate bias in collection sampling influence model outcomes? *J Biogeogr* **35**: 105–16.

Lombardo U, Iriarte J, Hilbert L, *et al.* 2020. Early Holocene crop cultivation and landscape modification in Amazonia. *Nature* **581**: 190–3.

Lopes AA, Chioca B, Musquiari B, *et al.* 2019. Unnatural spirocyclic oxindole alkaloids biosynthesis in Uncaria guianensis. *Sci Rep* **9**: 1–8.

López-Fernández H and Albert JS. 2011. Six. Paleogene Radiations. In: Historical biogeography of Neotropical freshwater fishes. University of California Press.

Lovejoy NR, Bermingham E, and Martin AP. 1998. Marine incursion into South America. *Nature* **396**: 421–2.

Luebert F and Weigend M. 2014. Phylogenetic insights into Andean plant diversification. *Front Ecol Evol* **2**: 27.

Luize BG, Magalhães JLL, Queiroz H, *et al.* 2018. The tree species pool of Amazonian wetland forests: Which species can assemble in periodically waterlogged habitats? *PLoS One* **13**: e0198130.

Lundberg JG, Lewis WM, Saunders JF, and Mago-Leccia F. 1987. A major food web component in the Orinoco River channel: evidence from planktivorous electric fishes. *Science* **237**: 81–3.

Lundberg JG, Marshall LG, Guerrero J, *et al.* 1998. The stage for Neotropical fish diversification: a history of tropical South American rivers. *Phylogeny Classif Neotrop fishes* **27**: 13–48.

Lundberg JG, Sabaj Pérez MH, Dahdul WM, and Aguilera OA. 2009. The Amazonian neogene fish fauna. *Amaz Landsc Species Evol A look into past*: 281–301.

Lynch Alfaro JW, Boubli JP, Paim FP, *et al.* 2015. Biogeography of squirrel monkeys (genus Saimiri): South-central Amazon origin and rapid pan-Amazonian diversification of a lowland primate. *Mol Phylogenet Evol* **82**: 436–54.

Macfoy C, Danosus D, Sandit R, et al. 2005. Alkaloids of anuran skin: Antimicrobial function? Zeitschrift fuer Naturforschung 60: 932–937.

Madriñán S, Cortés AJ, and Richardson JE. 2013. Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Front Genet* **4**: 192.

Magallón S, Gómez-Acevedo S, Sánchez-Reyes LL, and Hernández-Hernández T. 2015. A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytol* **207**: 437–53.

Magurran AE and McGill BJ. 2011. Biological diversity: frontiers in measurement and assessment. Oxford University Press.

Mahé F, Vargas C de, Bass D, *et al.* 2017. Parasites dominate hyperdiverse soil protist communities in Neotropical rainforests. *Nat Ecol \& Evol* **1**: 1–8.

Malhi Y, Roberts JT, Betts RA, *et al.* 2008. Climate change, deforestation, and the fate of the Amazon. *Science* **319**: 169–72.

Marichal R, Praxedes C, Decaëns T, *et al.* 2017. Earthworm functional traits, landscape degradation and ecosystem services in the Brazilian Amazon deforestation arc. *Eur J Soil Biol* **83**: 43–51.

Marshall LG, Webb SD, Sepkoski JJ, and Raup DM. 1982. Mammalian evolution and the great American interchange. *Science* **215**: 1351–7.

Martínez C, Madriñán S, Zavada M, and Alberto Jaramillo C. 2013. Tracing the fossil pollen record of Hedyosmum (Chloranthaceae), an old lineage with recent Neotropical diversification. *Grana* **52**: 161–80.

Mason CC, Romans BW, Stockli DF, *et al.* 2019. Detrital zircons reveal sea-level and hydroclimate controls on Amazon River to deep-sea fan sediment transfer. *Geology* **47**: 563–7.

McAllister CT, Bursey CR, and Freed PS. 2010. Helminth parasites of amphibians and reptiles from the Ucayali region, Peru. *J Parasitol* **96**: 444–7.

McGugan JR, Byrd GD, Roland AB, *et al.* 2016. Ant and mite diversity drives toxin variation in the Little Devil Poison frog. *J Chem Ecol* **42**: 537–51.

McKinney ML. 1997. Extinction Vulnerability and Selectivity: Combining Ecological and Paleontological Views. *Annu Rev Ecol Syst* **28**: 495–516.

Meffe GK and Carroll CR. 1994. Principles of conservation biology (S Associates, Ed). Massachusetts, USA: Sinauer Associates.

Mejia-Velasquez PJ, Dilcher DL, Jaramillo CA, *et al.* 2012. Palynological composition of a Lower Cretaceous South American tropical sequence: climatic implications and diversity comparisons with other latitudes. *Am J Bot* **99**: 1819–27.

Melo BF, Ochoa LE, Vari RP, and Oliveira C. 2016. Cryptic species in the Neotropical fish genus Curimatopsis (Teleostei, Characiformes). *Zool Scr* **45**: 650–8.

Menezes RST, Lloyd MW, and Brady SG. 2020. Phylogenomics indicates Amazonia as the major source of Neotropical swarm-founding social wasp diversity. *Proc R Soc B* **287**: 20200480.

Mittermeier RA, Mittermeier CG, Brooks TM, *et al.* 2003. Wilderness and biodiversity conservation. *Proc Natl Acad Sci* **100**: 10309–13.

Molina-Venegas R, Rodríguez MÁ, Pardo-de-Santayana M, *et al.* 2021. Maximum levels of global phylogenetic diversity efficiently capture plant services for humankind. *Nat Ecol Evol*.

Montes C, Silva CA, Bayona GA, *et al.* 2021. A Middle to Late Miocene Trans-Andean Portal: Geologic Record in the Tatacoa Desert . *Front Earth Sci* **8**: 643.

Montoya E, Lombardo U, Levis C, *et al.* 2020. Human Contribution to Amazonian Plant Diversity: Legacy of Pre-Columbian Land Use in Modern Plant Communities

Mueller RC, Rodrigues JLM, Nüsslein K, and Bohannan BJM. 2016. Land use change in the Amazon rain forest favours generalist fungi. *Funct Ecol* **30**: 1845–53.

Naka LN and Brumfield RT. 2018. The dual role of Amazonian rivers in the generation and maintenance of avian diversity. *Sci Adv* **4**: eaar8575.

Nazareno AG, Dick CW, and Lohmann LG. 2017. Wide but not impermeable: Testing the riverine barrier hypothesis for an Amazonian plant species. *Mol Ecol* **26**: 3636–48.

Nazareno AG, Dick CW, and Lohmann LG. 2019. A Biogeographic barrier test reveals a strong genetic structure for a canopy-emergent amazon tree species. *Sci Rep* **9**: 1–11.

Nazareno AG, Dick CW, and Lohmann LG. 2019. Tangled banks: A landscape genomic evaluation of Wallace's Riverine barrier hypothesis for three Amazon plant species. *Mol Ecol* **28**: 980–97.

Nazareno AG, Knowles LL, Dick CW, and Lohmann LG. 2021. By Animal, Water, or Wind: Can Dispersal Mode Predict Genetic Connectivity in Riverine Plant Species? *Front Plant Sci* **12**: 626405.

Nelson BW, Ferreira CAC, Silva MF da, and Kawasaki ML. 1990. Endemism centres, refugia and botanical collection density in Brazilian Amazonia. *Nature* **345**: 714–6.

Odling-Smee FJ, Laland KN, and Feldman MW. 2013. Niche construction: the neglected process in evolution (MPB-37). Princeton university press.

Oliveros CH, Field DJ, Ksepka DT, *et al.* 2019. Earth history and the passerine superradiation. *Proc Natl Acad Sci* **116**: 7916–25.

Orme AR. 2007. Tectonism, climate, and landscape change. *Phys Geogr South Am*: 23–44.

Padilla-González GF, Diazgranados M, and Costa FB Da. 2017. Biogeography shaped the metabolome of the genus Espeletia: A phytochemical perspective on an Andean adaptive radiation. *Sci Rep* **7**: 1–11.

Palin OF, Eggleton P, Malhi Y, *et al.* 2011. Termite diversity along an Amazon--Andes elevation gradient, Peru. *Biotropica* **43**: 100–7.

Paolillo A and Linares OJ. 2007. Nuevos cocodrilos sebecosuchia del cenozoico suramericano (Mesosuchia: Crocodylia). *Paleobiol Neotrop* **3**: 1–25.

Papadopoulou A and Knowles LL. 2016. Toward a paradigm shift in comparative phylogeography driven by trait-based hypotheses. *Proc Natl Acad Sci* **113**: 8018–24.

Parolin P, Wittmann F, Ferreira L V, and others. 2013. Fruit and seed dispersal in Amazonian floodplain trees--a review. *Ecotropica* **19**: 15–32.

Parra G De La, Jaramillo C, and Dilcher D. 2008. Paleoecological changes of spore producing plants through the Cretaceous-Paleocene boundary in Colombia. In: Palynology. Amer assoc stratigraphic palynologists foundation c/o vaughn m Bryant, jr, palnology laboratory.

Paz A, Ibáñez R, Lips KR, and Crawford AJ. 2015. Testing the role of ecology and life history in structuring genetic variation across a landscape: A trait-based phylogeographic approach. *Mol Ecol* **24**: 3723–37.

Pérez-Escobar OA, Gottschling M, Chomicki G, *et al.* 2017. Andean mountain building did not preclude dispersal of lowland epiphytic orchids in the Neotropics. *Sci Rep* **7**: 1–10.

Perrigo A, Hoorn C, and Antonelli A. 2020. Why mountains matter for biodiversity. *J Biogeogr* **47**: 315–25.

Philippe G and Angenot L. 2005. Recent developments in the field of arrow and dart poisons. *J Ethnopharmacol* **100**: 85–91.

Pinna M, Zuanon J, Rapp Py-Daniel L, and Petry P. 2018. A new family of neotropical freshwater fishes from deep fossorial Amazonian habitat, with a reappraisal of morphological characiform phylogeny (Teleostei: Ostariophysi). *Zool J Linn Soc* **182**: 76–106.

Plotkin MJ. 1988. The outlook for new agricultural and industrial products from the tropics. National Academy Press, Washington, DC.

Polato NR, Gill BA, Shah AA, *et al.* 2018. Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains. *Proc Natl Acad Sci* **115**: 12471–6.

Pouchon C, Fernández A, Nassar JM, *et al.* 2018. Phylogenomic Analysis of the Explosive Adaptive Radiation of the Espeletia Complex (Asteraceae) in the Tropical Andes. *Syst Biol* **67**: 1041–60.

Poulsen CJ, Ehlers TA, and Insel N. 2010. Onset of convective rainfall during gradual late Miocene rise of the central Andes. *Science* **328**: 490–3.

PPBio. 2005. Programa de pesquisa em biodiversidadehttps://ppbio.inpa.gov.br/en/home.

Prado JL, Martinez-Maza C, and Alberdi MT. 2015. Megafauna extinction in South America: A new chronology for the Argentine Pampas. *Palaeogeogr Palaeoclimatol Palaeoecol* **425**: 41–9.

Prestes-Carneiro G, Béarez P, Bailon S, *et al.* 2016. Subsistence fishery at Hatahara (750–1230 CE), a pre-Columbian central Amazonian village. *J Archaeol Sci Reports* **8**: 454–62.

Puckett DO. 2018. A Survey of Ant-Associated Fungal Diversity in Canopy Bromeliads from the Ecuadorian Amazon.

Pupim FN, Sawakuchi AO, Almeida RP de, *et al.* 2019. Chronology of Terra Firme formation in Amazonian lowlands reveals a dynamic Quaternary landscape. *Quat Sci Rev* **210**: 154–63.

Purvis A, Gittleman JL, Cowlishaw G, and Mace GM. 2000. Predicting extinction risk in declining species. *Proc R Soc London Ser B Biol Sci* **267**: 1947–52.

Quintero I and Jetz W. 2018. Global elevational diversity and diversification of birds. *Nature* **555**: 246–50.

Rahbek C, Borregaard MK, Antonelli A, *et al.* 2019. Building mountain biodiversity: Geological and evolutionary processes. *Science* **365**: 1114–9.

RAISG. 2020. Amazonian Network of Georeferenced Socio-Environmental Informationhttps://www.amazoniasocioambiental.org/en/ . Viewed

Rangel TF, Edwards NR, Holden PB, *et al.* 2018. Modeling the ecology and evolution of biodiversity: Biogeographical cradles, museums, and graves. *Science* **361**.

Räsänen M, Neller R, Salo J, and Jungner H. 1992. Recent and ancient fluvial deposition systems in the Amazonian foreland basin, Peru. *Geol Mag* **129**: 293–306.

Räsänen ME, Salo JS, Jungnert H, and Pittman LR. 1990. Evolution of the western Amazon lowland relief: impact of Andean foreland dynamics. *Terra Nov* **2**: 320–32.

Raup DM. 1986. Biological extinction in earth history. *Science* **231**: 1528–33.

Raven PH, Gereau RE, Phillipson PB, *et al.* 2020. The distribution of biodiversity richness in the tropics. *Sci Adv* **6**: eabc6228.

Reis A, Magne K, Massot S, *et al.* 2019. Amaryllidaceae alkaloids: identification and partial characterization of montanine production in Rhodophiala bifida plant. *Sci Rep* **9**: 1–11.

Reis RE, Albert JS, Dario F Di, *et al.* 2016. Fish biodiversity and conservation in South America. *J Fish Biol* **89**: 12–47.

Réjaud A, Rodrigues MT, Crawford AJ, *et al.* 2020. Historical biogeography identifies a possible role of Miocene wetlands in the diversification of the Amazonian rocket frogs (Aromobatidae: Allobates). *J Biogeogr* **47**: 2472–82.

Ribas CC, Aleixo A, Nogueira ACR, *et al.* 2012. A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. *Proc R Soc B Biol Sci* **279**: 681–9.

Ribas CC, Moyle RG, Miyaki CY, and Cracraft J. 2007. The assembly of montane biotas: linking Andean tectonics and climatic oscillations to independent regimes of diversification in Pionus parrots. *Proc R Soc B Biol Sci* **274**: 2399–408.

Richardson JE, Pennington RT, Pennington TD, and Hollingsworth PM. 2001. Rapid diversification of a species-rich genus of neotropical rain forest trees. *Science* **293**: 2242–5.

Richey JE, Nobre C, and Deser C. 1989. Amazon River Discharge and Climate Variability: 1903 to 1985. *Science* **246**: 101–3.

Ricklefs RE and Schluter D. 1993. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press Chicago.

Riff D, R. Romano PS, Oliveira GR, and Aguilera OA. 2010. Neogene crocodile and turtle fauna in northern South America. *Amaz Landsc Species Evol A look into past*: 259–80.

Ritter CD, Dunthorn M, Anslan S, *et al.* 2020. Advancing biodiversity assessments with environmental DNA: Long-read technologies help reveal the drivers of Amazonian fungal diversity. *Ecol Evol* **10**: 7509–24.

Roberts M. 1839. Sketches of the animal and vegetable productions of America. London,: J.W. Parker,.

Rohrmann A, Sachse D, Mulch A, *et al.* 2016. Miocene orographic uplift forces rapid hydrological change in the southern central Andes. *Sci Rep* **6**: 1–7.

Roncal J, Kahn F, Millan B, *et al.* 2013. Cenozoic colonization and diversification patterns of tropical American palms: evidence from Astrocaryum (Arecaceae). *Bot J Linn Soc* **171**: 120–39.

Roosevelt AC. 2013. The Amazon and the Anthropocene: 13,000 years of human influence in a tropical rainforest. *Anthropocene* **4**: 69–87.

Rosser N, Shirai LT, Dasmahapatra KK, *et al.* 2021. The Amazon river is a suture zone for a polyphyletic group of co-mimetic heliconiine butterflies. *Ecography (Cop)* **44**: 177–87.

Rowe N and Speck T. 2005. Plant growth forms: an ecological and evolutionary perspective. *New Phytol* **166**: 61–72.

Roxo FF, Albert JS, Silva GSC, *et al.* 2014. Molecular phylogeny and biogeographic history of the armored Neotropical catfish subfamilies Hypoptopomatinae, Neoplecostominae and Otothyrinae (Siluriformes: Loricariidae). *PLoS One* **9**: e105564.

Rull V. 2008. Speciation timing and neotropical biodiversity: the Tertiary-Quaternary debate in the light of molecular phylogenetic evidence. *Mol Ecol* **17**: 2722–9.

Rull V. 2011. Origins of Biodiversity. *Science* **331**: 398–9.

Rull V. 2020. Neotropical Diversification: Historical Overview and Conceptual Insights BT - Neotropical Diversification: Patterns and Processes. In: Rull V, Carnaval AC (Eds). Cham: Springer International Publishing.

Rull V. 2020. Neotropical diversification: historical overview and conceptual insights. *Neotrop Diversif patterns Process*: 13–49.

Ruokolainen K, Tuomisto H, Vormisto J, and Pitman N. 2002. Two Biases in Estimating Range Sizes of Amazonian Plant Species. *J Trop Ecol* **18**: 935–42.

Sakschewski B, Bloh W Von, Boit A, *et al.* 2016. Resilience of Amazon forests emerges from plant trait diversity. *Nat Clim Chang* **6**: 1032–6.

Salas-Gismondi R, Flynn JJ, Baby P, *et al.* 2015. A Miocene hyperdiverse crocodylian community reveals peculiar trophic dynamics in proto-Amazonian mega-wetlands. *Proc R Soc B Biol Sci* **282**: 20142490.

Salgado-Maldonado G, Novelo-Turcotte MT, Caspeta-Mandujano JM, *et al.* 2016. Host specificity and the structure of helminth parasite communities of fishes in a Neotropical river in Mexico. *Parasite* **23**.

Sanchez-Villagra MR, Aguilera O, and Carlini A. 2010. Urumaco and Venezuelan Paleontology. The Fossil Record of the Northern Neotropics. Bloomington and Indianapolis , USA: Indiana University Press.

Santos CD, Sarmento H, Miranda FP de, *et al.* 2019. Uncovering the gene machinery of the Amazon River microbiome to degrade rainforest organic matter. *bioRxiv*: 585562.

Santos M da CF, Ruffino ML, and Farias IP. 2007. High levels of genetic variability and panmixia of the tambaqui Colossoma macropomum (Cuvier, 1816) in the main channel of the Amazon River. *J Fish Biol* **71**: 33–44.

Santos-Júnior CD, Kishi LT, Toyama D, *et al.* 2017. Metagenome sequencing of prokaryotic microbiota collected from rivers in the upper Amazon basin. *Genome Announc* **5**.

Saporito RA, Spande TF, Garraffo HM, and Donnelly MA. 2009. Arthropod alkaloids in poison frogs: a review of the dietary hypothesis. *Heterocycles* **79**: 277–97.

Saporito RA, Donnelly MA, Spande TF, Garraffo HM. 2011. A review of chemical ecology in poison frogs. Chemoecol 21: 1–10.

Scheyer TM, Aguilera OA, Delfino M, *et al.* 2013. Crocodylian diversity peak and extinction in the late Cenozoic of the northern Neotropics. *Nat Commun* **4**: 1907.

Schultz ED, Burney CW, Brumfield RT, *et al.* 2017. Systematics and biogeography of the Automolus infuscatus complex (Aves; Furnariidae): Cryptic diversity reveals western Amazonia as the origin of a transcontinental radiation. *Mol Phylogenet Evol* **107**: 503–15.

Schultz ED, Pérez-Emán J, Aleixo A, *et al.* 2019. Diversification history in the Dendrocincla fuliginosa complex (Aves: Dendrocolaptidae): insights from broad geographic sampling. *Mol Phylogenet Evol* **140**: 106581.

Seraphim N, Kaminski LA, Devries PJ, *et al.* 2018. Molecular phylogeny and higher systematics of the metalmark butterflies (Lepidoptera: Riodinidae). *Syst Entomol* **43**: 407–25.

Shah AA, Gill BA, Encalada AC, *et al.* 2017. Climate variability predicts thermal limits of aquatic insects across elevation and latitude. *Funct Ecol* **31**: 2118–27.

Shahabuddin G and Ponte CA. 2005. Frugivorous butterfly species in tropical forest fragments: correlates of vulnerability to extinction. *Biodivers \& Conserv* **14**: 1137–52.

Shepard GH and Ramirez H. 2011. "Made in Brazil": Human Dispersal of the Brazil Nut (Bertholletia excelsa, Lecythidaceae) in Ancient Amazonia1. *Econ Bot* **65**: 44–65.

Silva JMC Da, Rylands AB, and Fonseca GAB Da. 2005. The Fate of the Amazonian Areas of Endemism. *Conserv Biol* **19**: 689–94.

Silva SM, Peterson AT, Carneiro L, *et al.* 2019. A dynamic continental moisture gradient drove Amazonian bird diversification. *Sci Adv* **5**: eaat5752.

Sleen P van der and Albert JS. 2017. Field guide to the fishes of the Amazon, Orinoco, and Guianas. Princeton University Press.

Sobral-Souza T, Lima-Ribeiro MS, and Solferini VN. 2015. Biogeography of Neotropical Rainforests: past connections between Amazon and Atlantic Forest detected by ecological niche modeling. *Evol Ecol* **29**: 643–55.

Sombroek W. 2000. Amazon landforms and soils in relation to biological diversity. *Acta Amaz* **30**: 81.

Soulé ME. 1985. What is conservation biology? *Bioscience* **35**: 727–34.

Souza-Filho JP, Souza RG, Hsiou AS, *et al.* 2018. A new caimanine (Crocodylia, Alligatoroidea) species from the Solimões Formation of Brazil and the phylogeny of Caimaninae. *J Vertebr Paleontol* **38**: e1528450.

Stebbins GL. 1974. Flowering Plants: Evolution Above the Species Level (Harvard University Press, Ed). Cambridge, Massachusetts: Belknap Press.

Stehli FG and Webb SD. 1985. The great American biotic interchange. Springer Science & Business Media.

Stenseth NC. 1984. The Tropics: Cradle or Museum? *Oikos* **43**: 417–20.

Stork NE. 2018. How many species of insects and other terrestrial arthropods are there on Earth? *Annu Rev Entomol* **63**: 31–45.

Stouffer PC, Jirinec V, Rutt CL, *et al.* 2021. Long-term change in the avifauna of undisturbed Amazonian rainforest: ground-foraging birds disappear and the baseline shifts (J Lawler, Ed). *Ecol Lett* **24**: 186–95.

Tedesco PA, Beauchard O, Bigorne R, *et al.* 2017. A global database on freshwater fish species occurrence in drainage basins. *Sci Data* **4**: 170141.

Terborgh J and Andresen E. 1998. The composition of Amazonian forests: patterns at local and regional scales. *J Trop Ecol*: 645–64.

Ter-Steege H, Pitman NCA, Phillips OL, *et al.* 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* **443**: 444–7.

Ter-Steege H, Prado PI, Lima RAF de, *et al.* 2020. Biased-corrected richness estimates for the Amazonian tree flora. *Sci Rep* **10**: 10130.

Testo WL, Sessa E, and Barrington DS. 2019. The rise of the Andes promoted rapid diversification in Neotropical Phlegmariurus (Lycopodiaceae). *New Phytol* **222**: 604–13.

Thatcher VE. 2006. Amazon fish parasites. Pensoft Publishers.

Thode VA, Sanmartín I, and Lohmann LG. 2019. Contrasting patterns of diversification between Amazonian and Atlantic forest clades of Neotropical lianas (Amphilophium, Bignonieae) inferred from plastid genomic data. *Mol Phylogenet Evol* **133**: 92–106.

Thom G and Aleixo A. 2015. Cryptic speciation in the white-shouldered antshrike (Thamnophilus aethiops, Aves--Thamnophilidae): The tale of a transcontinental radiation across rivers in lowland Amazonia and the northeastern Atlantic Forest. *Mol Phylogenet Evol* **82**: 95–110.

Thom G, Amaral FR Do, Hickerson MJ, *et al.* 2018. Phenotypic and Genetic Structure Support Gene Flow Generating Gene Tree Discordances in an Amazonian Floodplain Endemic Species (A Leache, Ed). *Syst Biol* **67**: 700–18.

Thom G, Xue AT, Sawakuchi AO, *et al.* 2020. Quaternary climate changes as speciation drivers in the Amazon floodplains. *Sci Adv* **6**: eaax4718.

Tokuyama T and Daly JW. 1983. Steroidal alkaloids (batrachotoxins and 4$β$-hydroxybatrachotoxins),“indole alkaloids”(calycanthine and chimonanthine) and a piperidinyldipyridin. *Tetrahedron* **39**: 41–7.

Tuomisto H, Doninck J Van, Ruokolainen K, *et al.* 2019. Discovering floristic and geoecological gradients across Amazonia. *J Biogeogr* **46**: 1734–48.

Tuomisto H, Zuquim G, and Cárdenas G. 2014. Species richness and diversity along edaphic and climatic gradients in Amazonia. *Ecography (Cop)* **37**: 1034–46.

Ulloa CU and Neill DA. 2006. Phainantha shuariorum (Melastomataceae), una especie nueva de la Cordillera del Cóndor, Ecuador, disyunta de un género guayanés. *Novon A J Bot Nomencl* **16**: 281–5.

Urban MA, Nelson DM, Jiménez-Moreno G, *et al.* 2010. Isotopic evidence of C4 grasses in southwestern Europe during the Early Oligocene--Middle Miocene. *Geology* **38**: 1091–4.

Vacher J, Chave J, Ficetola FG, *et al.* 2020. Large-scale DNA-based survey of frogs in Amazonia suggests a vast underestimation of species richness and endemism. *J Biogeogr* **47**: 1781–91.

Valen L Van. 1973. A new evolutionary law. *Evol Theory* **30**: 1–30.

Vargas OM, Ortiz EM, and Simpson BB. 2017. Conflicting phylogenomic signals reveal a pattern of reticulate evolution in a recent high-Andean diversification (Asteraceae: Astereae: Diplostephium). *New Phytol* **214**: 1736–50.

Vasconcelos TNC, Alcantara S, Andrino CO, *et al.* 2020. Fast diversification through a mosaic of evolutionary histories characterizes the endemic flora of ancient Neotropical mountains. *Proc R Soc B Biol Sci* **287**: 20192933.

Vellend M and Orrock JL. 2009. Ecological and genetic models of diversity: lessons across disciplines. *theory Isl Biogeogr revisited Princet Univ Press Princet*: 439–61.

Vianna RT and Boeger WA. 2019. Neotropical Monogenoidea. 60. Two new species of Gyrodactylus (Monogenoidea: Gyrodactylidae) from the armored-catfish, Pareiorhaphis parmula Pereira (Loricariidae) and from the cascarudo, Callichthys callichthys (Linnaeus) (Callichthyidae) from Brazil. *Zootaxa* **4551**: 87.

Vicentini A, Barber JC, Aliscioni SS, *et al.* 2008. The age of the grasses and clusters of origins of C4 photosynthesis. *Glob Chang Biol* **14**: 2963–77.

Vieira R and Höfer H. 2021. Butterflies of the Amazonhttps://www.amazonian-butterflies.net. Viewed

Voelker G, Marks BD, Kahindo C, *et al.* 2013. River barriers and cryptic biodiversity in an evolutionary museum. *Ecol Evol* **3**: 536–45.

Vogt RC and Bernhard R. 2003. Biodiversidade e biogeografia de répteis e anfíbios da Amazônia.

Wallace AR. 1852. On the Monkeys of the Amazon. *Ann Mag Nat Hist* **14**: 451–4.

Wang X, Edwards RL, Auler AS, *et al.* 2017. Hydroclimate changes across the Amazon lowlands over the past 45,000 years. *Nature* **541**: 204–7.

Watling J, Iriarte J, Mayle FE, *et al.* 2017. Impact of pre-Columbian "geoglyph" builders on Amazonian forests. *Proc Natl Acad Sci* **114**: 1868–73.

Webb SD. 1991. Ecogeography and the great American interchange. *Paleobiology*: 266–80.

Weldon PJ, Kramer M, Gordon S, et al. 2006. A common pumiliotoxin from poison frogs exhibits enantioselective toxicity against mosquitoes. P Natl Acad Sci USA 103: 17818–17821.

Wesselingh FP and Ramos M-IF. 2010. Amazonian Aquatic Invertebrate Faunas (Mollusca, Ostracoda) and their Development over the Past 30 Million Years. In: Amazonia: Landscape and Species Evolution. Oxford, UK: Wiley-Blackwell Publishing Ltd.

Wesselingh FP and Salo JA. 2006. A Miocene perspective on the evolution of the Amazonian biota. *Scr Geol* **133**: 439–58.

Wilkinson MJ, Marshall LG, Lundberg JG, and Kreslavsky MH. 2010. Megafan environments in northern South America and their impact on Amazon Neogene aquatic ecosystems. *Amaz Landsc species Evol a look into past*: 162–84.

Winemiller KO and Jepsen DB. 1998. Effects of seasonality and fish movement on tropical river food webs. *J Fish Biol* **53**: 267–96.

Winemiller KO, McIntyre PB, Castello L, *et al.* 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* **351**: 128–9.

Wing SL, Herrera F, Jaramillo CA, *et al.* 2009. Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of Neotropical rainforest. *Proc Natl Acad Sci* **106**: 18627–32.

Wittmann F, Householder E, Piedade MTF, *et al.* 2013. Habitat specifity, endemism and the neotropical distribution of Amazonian white-water floodplain trees. *Ecography (Cop)* **36**: 690–707.

WWF. 2016. Living planet: Report 2016: Risk and resilience in a new era. Gland, Switzerland.

11. GLOSSARY

Abiotic. Non-living physical and chemical aspects of the environment that affect living organisms and ecosystem functions.

Adaptation (*n.*) Organismal traits or phenotypes that have evolved by the process of *natural selection.* Adaptations allow organisms to become better adjusted to the environments in which they live. Adaptations can represent any aspect of organismal design, including morphology, body size, color, physiology, or behavior.

Adaptation (*v.*) The process by which organismal phenotypes change from ancestors to descendants, as a result of *natural selection*. An evolutionary process by which natural selection changes the frequencies (proportions) of alternative genes within a population. The process of becoming *adapted.*

Alkaloid. A class of basic, naturally occurring, nitrogen-containing organic compounds. Alkaloids are produced by a large variety of organisms including bacteria, fungi, plants, and animals. Alkaloids have a wide range of pharmacological properties, and physiological effects on animals and plants.

Allochemical. A chemical produced by a living organism, exerting a detrimental physiological effect on the individuals of another species when released into the environment.

Allopatric speciation. The formation of new species following the geographic isolation of populations by a barrier to migration and gene flow, i.e., geographic speciation. Examples include barriers formed by the rise of mountains, changing river courses, shorelines, and climate zones. Compare with *Ecological Speciation.*

Amazonia. A biogeographic region covering about 8.4 million sq km of northern South America, including the lowland Amazon and Orinoco river basins and adjacent upland areas of the Guiana and Brazilian Shields. Amazonia encompasses the *Amazon River Basin* covering about 7 million sq km, and the *Amazon Rainforest* covering about 5.5 million sq km in nine countries.

Biodiversity. The variety and variability of Life on Earth, often measured at the genetic, species, and ecosystem levels. Some commonly used biodiversity metrics include: *Species Richness* (number of species), *Species Endemism* (number of species restricted to a geographic area), *Functional Diversity* (range of physiological and ecological processes within and among species), *Genetic Diversity* (range of genetic differences within and among species), *Phylogenetic Diversity* (sum of lengths of all evolutionary branches among species), and *Taxic Diversity* (numbers of higher taxa like genera or families).

Biota. All the plants and animal species of a region. *Flora:* all the plant species of a region. *Fauna:* all the animal species of a region.

Biotic. Biotic processes are those carried out by living organisms. Some examples include biotic interactions (when multiple species interact ecologically), biotic interchange (when species are exchanged across regions, often in response to the emergence of new corridors), and biotic diversification (the process that leads to the generation of new species).

Biotic facilitation. Biotic interactions (e.g. symbiosis, predation, parasitism, etc.) where the presence of species in a local assemblage favors the establishment or persistence of other species in that assemblage.

C4 plants. C4 carbon fixation is a photosynthetic process in some plants, where a four-carbon molecule is the first product of carbon fixation. It is one of three known processes for carbon fixation. Some 3% of all plants use this process, especially the grass family Poaceae.

Carnivorous. Refers to an animal or plant whose food and energy requirements derive from animal tissue.

Cis- and trans- Andean. Cis-Andean groups are those distributed to the East of the Andes, on the Atlantic Ocean side. Trans-Andean groups are distributed to the West and North of the Andes, on the Pacific Ocean and Carribean Sea side.

Clade. A group that is composed of a common ancestor and all its descendant species. A branch of the Tree of Life.

Court Jester Hypothesis. The hypothesis that abiotic (non-living) processes, such as climate, tectonics, and extraterrestrial events, are the main drivers of evolutionary change and the origin of new species and higher taxa. Contrasted with *Red Queen Hypothesis*.

Cryptic diversity. Two or more species are ‘cryptic’ if they are, or have been, classified as a single species because they are superficially indistinguishable.

Detritivorous. Living organisms that obtain nutrients through the consumption of decomposing plants and animals, or their excrements (faeces).

Ecological Speciation. The formation of new species by natural selection under diverging environmental conditions. Also known as sympatric speciation. Compare with *Allopatric speciation.*

Ecosystem engineers. Organisms able to create or contribute to the modification, maintenance, or destruction of habitats or other ecological structure. Ecosystem engineers may create and maintain the health and stability of both abiotic and biotic aspects of the environment.

Evolutionary arms race. A struggle between competing sets of co-evolving genes, traits, or species, that develop adaptations and counter-adaptations against each other, resembling a human military arms race.

Evolutionary lineage (or lineage). A continuous line of descent; a series of organisms connected by reproduction by parent to offspring. An ancestor-descendant sequence of populations, cells, or genes. All evolutionary lineages that exist and have existed in our planet are connected through a single evolutionary Tree of Life, because all organisms on Earth evolved from a single common ancestor.

Extinction. The process by which a species or higher-order group becomes extinct, that is, has no living representatives.

Extirpation. Local extinction, when a species ceases to exist in a geographic area while persisting elsewhere.

Interfluve. Landform area between adjacent river valleys. Plural form = interfluvia.

Facilitation. Species interactions that benefit at least one species and cause harm to neither. Facilitations can be categorized as mutualisms, in which both species benefit, or commensalisms, in which one species benefits and the other is unaffected.

Megafan. A sediment pile deposited by stream flows that originate from a single source in mountain range.

Megafauna. Large or giant animals of an area, habitat, or geological period. The most common thresholds used are weight over 40 kilograms (90 lb) or 44 kilograms (100 lb).

Metagenomics. A molecular technique that is able to extract and analyze small amounts of genetic material obtained directly from environmental samples (such as soil, water, faeces, skin), with the goal of producing a profile of diversity from the analysed samples.

Neotropical. Belonging to the Neotropical realm or ecozone. The Neotropical realm includes South America, Central America, the Caribbean islands, large portions of Mexico, and southern Florida (United States).

Omnivorous. An organism that eats food of various origins (fungi, plant and animal).

Pebas megawetland system. A long lived, large-scale aquatic setting at sea level that occupied western Amazonia during the Miocene from ca. 22 to 10 million years ago.

Phenotype. The set of observable characteristics of an individual, including not only its physical appearance but also its physiological abilities and behavior. Phenotypes are the result of the interactions between the genetic make-up of individuals (the genotype) and the environment in which they live.

Red Queen Hypothesis. The hypothesis that biotic (living) processes and species interactions, such as competition, predation, and parasitism, are the main drivers of evolutionary change, and that species must constantly adapt and evolve in order to survive and avoid extinction. Contrasted with *Court Jester Hypothesis.*

Pleistocene Refugia Hypothesis. The hypothesis proposed by Jürgen Haffer that the high diversity of lowland Amazonian species was generated by speciation and dispersal accompanying episodic contraction and expansion of forest refuges during the glacial cycles ca. 2.6 to 0.01 million years ago.

Seasonally Dry Diagonal. Open vegetation biomes that extend diagonally across a latitudinal range in South America, including the Caatinga, Cerrado, Dry Forests, and Gran Chaco (Figure 1).

Speciation. The origination of a new species.

Speciation rates. The rate at which new species originate.

Speciation richness. The number of species in an area or taxonomic group.

Sympatric speciation. Speciation is said to be sympatric when it happens in the absence of evident geographical barriers, that is, when an ancestral species diversifies into two species that coexist in the same geographical region. Sympatric speciation is often observed in association to changes in breeding or feeding behavior.

Species. A lineage that has a distinct and unique evolutionary origin, and which can be differentiated from other such lineages by the genetic, physical, behavioral, or ecological characteristics of its individuals.

Taxon. A taxonomic group of any rank, such as a species, family, or class. **Taxa** is the plural of taxon.

Taxonomy. The science of naming, defining, and classifying groups of biological organisms.

Trait. Any morphological, physiological, or phenological heritable feature measurable at the level of the individual.