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. Guayasamin¹, Camila C. Ribas², Ana Carolina Carnaval³, Juan D. Carrillo⁴, Carina Hoorn⁵, Lúcia G. Lohmann⁶, Douglas Riff⁷, Carmen Ulloa Ulloa⁸, & James S. Albert⁹.

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
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.
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ACRONYMS AND ABBREVIATIONS

c.a. = *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. 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 present 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.
Chapter 2

Science Panel for the Amazon

Guayasamin et al.

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 km² 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 km² (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 m² 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).

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BOX 1. Adaptaions 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 interfluvies 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; Dátillo 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 Carroll, 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 km² (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-American 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 proboscidiants 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).

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**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 brasiensis* 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 (Bertholletia 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).
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).

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.

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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
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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.