Chapter 2 In Brief

Evolution of Amazonian biodiversity

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THE AMAZON WE WANT
Science Panel for the Amazon

Evolution of Amazonian biodiversity

Juan M. Guayasamin[a], Camila C. Ribas[b], Ana Carolina Carnaval[c], Juan D. Carrillo[d], Carina Hoorn[e], Lúcia G. Lohmann[f], Douglas Riff[g], Carmen Ulloa Ulloa[h], James S. Albert[i]

Key Messages & Recommendations

1) The Amazon represents the greatest concentration of biodiversity on Earth, with about 10% of all named vascular plants and vertebrate species, providing essential genetic, ecological, and economic resources for Amazonian people and global society as a whole.
2) Amazonian biodiversity is heterogeneously distributed among many distinct ecosystems and environments, each harboring unique ecological and evolutionary processes. Biodiversity patterns (like richness and endemicity) are often idiosyncratic; each region and taxonomic group must therefore be studied individually.
3) Amazonian biodiversity derived from natural processes operating over immense time periods (tens of millions of years) and across the vast spatial scale of the entire South American continent.
4) Preserving Amazonian biodiversity depends on maintaining the evolutionary and ecological processes that generated it. Diversification of local biota has taken place in response not only to changes in landscapes and climates, but also to the presence of other species. Amazonian biodiversity begets more biodiversity, locally and regionally.
5) Understanding and preserving the Amazon requires decade-level financial investments and political support for Amazonian biodiversity science, prioritizing local scientific collections and research and education institutions that enable the study of Amazonian biodiversity at multiple spatial and temporal scales. It also requires training the next generation of Amazonian scientists and conservationists.

Abstract This chapter reviews the evolutionary history of the Amazon's terrestrial and riverine ecosystems, involving geological and climatic events operating over millions of years and across the whole of continental South America. The chapter discusses the important roles of geographic barriers, habitat heterogeneity, climate change, and species interactions in generating and maintaining the most biodiverse ecosystems on Earth. This unique history produced heterogeneous environments and diverse habitats at multiple geographic scales, which altered the connections between populations and allowed for the accumulation of the most diverse biota on Earth.

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

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[a] Universidad San Francisco de Quito (USFQ), Instituto Biósfera-USFQ, Colegio de Ciencias Biológicas y Ambientales COCIBA, Laboratorio de Biología Evolutiva, campus Cumbayá, Diego de Robles s/n, Quito 170901, Ecuador, jmguayasamin@usfq.edu.ec

[b] Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo, 2936, Petrópolis, Manaus AM 69067-375, Brazil

[c] Biology Department, City College of New York, 160 Convent Ave, New York, NY 10031, USA; Ph.D. Program in Biology, The Graduate Center, CUNY, 365 5th Ave, New York NY 10016, USA

[d] CR2P, Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, 57 Rue Cuvier, 75005 Paris, France

[e] Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Spui 21, 1012 WX Amsterdam, The Netherlands

[f] Universidade de São Paulo, Instituto de Biociências, Departamento de Botânica, R. da Reitoria, 374, Cidade Universitária, Butantã, São Paulo SP 05508-220, Brazil

[g] Universidade Federal de Uberlândia, Instituto de Biologia, Laboratório de Paleontologia, Av. João Naves de Ávila 2121, Santa Mônica, Uberlândia, MG 38408-100, Brazil

[h] Missouri Botanical Garden, 4344 Shaw Blvd, St. Louis MO 63110, USA

[i] Department of Biology, University of Louisiana at Lafayette, 104 E University Ave, Lafayette LA 70504, USA

lianas, as well as epiphytes, herbaceous sedges, grasses, and colonial bamboos[1]. DNA studies suggest that flowering plants originated in the Lower Cretaceous (ca. 145–100 million years ago, or Ma)[2], and fossils indicate that flowering plants did not come to dominate tropical ecosystems until after the Upper Cretaceous (ca. 66 Ma)[3–7].

While some Amazonian lineages have truly ancient origins, dating back to the early Cenozoic or Cretaceous, most species that currently inhabit the Amazon emerged in the past few million years[8–13]. 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[8], and was influenced by many changes to the physical landscape along this period[14].

The last time the Amazon suffered a mass extinction (before the modern biodiversity crisis) was about 66 Ma, in association with the Cretaceous–Paleogene [K-Pg] asteroid impact event[7,15,16]. Most modern groups of Amazonian organisms diversified rapidly after this event, including birds[17,18], butterflies[19–21], and fishes[22,23]. Plant communities similar to those seen in modern Amazonian rainforests were first seen in the Paleocene (ca. 66–56 Ma[24,25]), with many plant lineages diversifying in the Eocene (ca. 58–41 Ma[26]). Rainforest plant diversity may have reached a pinnacle during the Eocene at a time when humid tropical climates predominated over most of South America[25,27–29]. Conspicuous elements of Neotropical rainforests in the Paleocene include members of key plant families such as certain herbs (e.g., Araceae, Zingiberaceae), shrubs (e.g., Malvaceae), lianas (e.g., Menispermaceae), and trees (e.g., palms, Lauraceae[24,30,31]).

The drier seasons and cooler climates of the early Oligocene (ca. 30 Ma) contributed to extensive vegetational changes in some parts of South America. The once continuous, broadly-distributed, humid South American rainforests were divided into two, the Amazon and Atlantic rainforests, due to the expansion of subtropical, open-woodland forests in central South America and the establishment of the Seasonally Dry Diagonal[32–37]. These vegetational changes coincided with the beginning of the uplift of the Mantiqueira Mountains of eastern Brazil, as well as the Northern Andes of Peru to Venezuela, both of which contributed to substantial changes in South American air currents and climate regimes. Increasingly drier climates and open savannah-type habitats were accompanied by substantial changes in species composition (e.g., palms), the origin of C4 grasses[38–40], and expansion of grasslands and open woodlands at the expense of closed-canopy forested habitats[41,42].

Continued uplift of the Northern Andes and increased orographic precipitation[43] during the Miocene (ca. 23–5.3 Ma) led to a profound reorganization of the river network, and the formation of the Pebas Mega-wetland system[3,44–46] (Figure 2.1). This system was composed of a vast (up to 1 million km^2 at times) lacustrine and swampy set of environments situated in lowland western Amazonia[46–48]. These seasonally and perennially-flooded forests included palms (i.e., *Grimsdalea*), ferns, and grasses (Poaceae)[42,45,49,50]. In addition, marine incursions from the Caribbean Sea south into western Amazonia allowed salt-tolerant and estuarine taxa to colonize the Pebas shorelines[47,50,51].

In the Late Miocene and Pliocene (ca. 10.0–4.5 Ma), overfilling of the western Amazonian sedimentary basins with Andean-derived sediments led to a renewed drainage reorganization and the onset of the modern transcontinental Amazon River. With the end of the Pebas System, most of the associated molluscan fauna became extinct, causing the first important extinction event of Pan-Amazonian crocodylians[52,53]. In stark contrast to the high turnover of mollusks and crocodilians, modern Amazonian fish fauna have remained largely unchanged at the genus level and higher (ca. 9–4.5 Ma[54]). The former Pebas wetland surfaces were colonized by many different lineages[14,55], in a process of upland forest expansion that is suggested to have continued until the Late Pleistocene[56].

Landscape changes also led to increased diversification of numerous plant lineages, such as the flowering plant genera *Inga* (Legumes[57]) and *Guatteria* (Annonaceae[58]). At around the same time, the Andean slopes were colonized by many plant lineages, including species of the Malvaceae[59], Arecaceae (i.e., palms[60]), and Chloranthaceae families (i.e., *Hedyosmum*[61]). In the Late Miocene to Pliocene (ca. 11–4 Ma[62]), 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[25].

The Neogene uplift of the Northern Andes (ca. 23–2.6 Ma) had profound effects on Amazonian landscapes, impacting lineage diversification and adaptation in both lowland (<250 m) and upland (>300 m) settings[54,62–64]. 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[65]. The uplift of the Northern Andes and its associated dynamic climate history were key drivers of the rapid radiation of Andean-centered plants[66–71] and animals[46,64,72]. Near the mountain tops, plants of the *páramo* ecosystem underwent one of the highest speciation rates ever recorded on Earth[61,73,74].

During the Quaternary (the last ca. 2.6 Ma), global climate cooling and ice-age cycles, together with regional geomorphological processes, altered important aspects of Amazonian landscapes. Alluvial megafans (sediment aprons of more than 10,000 km^2) extended from the Andes into Amazonia (e.g.,[75–77]), and floodplains varied in size according to changes in precipitation patterns and global sea levels[56].

The effects of these important climate and landscape changes on landscape and vegetation composition are yet to be fully understood. Direct studies of the sedimentary and fossil records[45,50,78], as well as climate models[79–81], suggest that general

Figure 2.1 Past diversity in the Amazon 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), while crocodiles and mollusks diversified with the onset of the mega-wetlands and declined with their demise (modified from [44]). Right: Reconstruction of the Amazonian landscape during the middle to late Miocene (16—7 Ma), highlighting the giant caiman *Purussaurus brasiliensis* preying on a *Trigodon toxodont*. Illustration by Orlando Grillo[44].

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[25,82,83].

Data from many sources do not support Pleistocene climate oscillations as the main driver in the formation of Amazonian biodiversity. Direct evidence from the fossil record indicates that most Amazonian plant and fish genera originated long before the Pleistocene[25,84,85]. Indeed, fossil Amazonian paleo-biotas were mostly composed of modern genera by the Miocene (c. 22–5 Ma), including grasses[42] and fishes[86]. Studies of pollen profiles in sediment cores indicate that savannah and open grassland ecosystems have never been widespread in lowland Amazonia[87–89]. Finally, DNA studies in many modern groups of plants and animals show relatively constant rates of diversification over the past several million years, without abrupt variation during the Pleistocene[12,90].

Nonetheless, some upland areas of the Guiana and Brazilian Shields in the Eastern Amazon did experience substantial changes in vegetation structure during the Quaternary[80,91], in the relative proportions of closed-canopy forests, open-canopy forests, and open woodland-savannas[80,83,92]. The effects of Pleistocene climate oscillations on diversification of Amazonian biotas are still incompletely understood. Continued studies on the evolutionary history of Amazonian organisms that characterize the region's distinct environments are crucial for improving models forecasting the effects of future anthropogenic climate change[93].

Assembling the Megadiverse Amazonian Biota Amazonian biodiversity was assembled through a unique and unrepeatable combination of processes that intermingle geological, climatic, and biological factors across broad spatial and temporal scales, involving taxa distributed across the whole of the South American continent and evolving over a period of tens of millions of years (Figure 2.1).

How old are Amazonian species? Amazonian species and higher taxa exhibit a broad range of evolutionary ages, such that the Amazon serves simultaneously as both an evolutionary cradle (i.e., a place of high species origination) and museum (i.e., species tend to accumulate through low rates of extinction). This pattern is observed in many taxonomic groups (e.g., plants[94], Amazonian rocket frogs or *Allobates*[95], and fishes[65]), although exceptions also exist [96,97]. At the same time, contrasting core-periphery patterns are observed in many Neotropical taxa[65,98–100]. Even though 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, represented by the sedimentary basins. While both young and old species are found in the shields and at the base of the Andes, species assemblages in the sedimentary basins are mostly composed of younger species.

Diversification dynamics 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[96,101,102]. Diversification in response to geographic barriers is one of the most widespread processes that facilitates speciation (allopatric speciation). 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[103–105]. This isolation led South America to harbor a peculiar and endemic mammalian megafauna[106]. The tectonics that elevated the Andes and caused the great environmental changes also elevated the terrestrial route that ended a long-lasting isolation of South America from other continents during most of the Cenozoic[107]. This isolation, which led South America to harbor a peculiar and endemic mammalian megafauna, ceased when the formation of the Isthmus of Panama facilitated biotic interchange between North and South America, through the event known as the Great American Biotic Interchange[108]. This connection had great implications for the historical assembly of Amazonian fauna and flora.

Reorganization of the river network prompted by Andean uplift also fragmented aquatic fauna of northwestern South America, leaving a clear signal on all major taxa[103]. Among families of freshwater fishes, the relative species diversity and biogeographic distributions were effectively modern by the Late Miocene. Changes in landscape connectivity have also strongly affected dispersal, gene flow, and biotic diversification within the Amazon. Large lowland Amazonian rivers, for instance, represent important geographic barriers for groups of primates (e.g.,[109,110]), birds[92,111], fishes[112], butterflies[113,114], wasps[115], and plants[116–119]. In birds, one of the best studied groups in Amazonia, it has been demonstrated that species from upland non-flooded forest have different ecological associations and evolutionary histories relative to the species that inhabit the floodplains and to those in open vegetation areas (Figure 2.2)[120,121,122]. However, 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 Amazon and the Negro, constitute effective barriers to dispersal for upland species of monkeys and birds (representing boundaries between closely related species of those groups[123]), these 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.,[54,124]).

Both terrestrial and aquatic Amazonian habitats have been profoundly affected by climate change, especially changing precipitation patterns and sea levels, over millions of years. 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[80,83,92,125]. The climate oscillations of the Pleistocene ice ages (2.6–0.01 Ma), in synergy with hunting by humans[126], reduced South American megafauna by ~80%[127,128]. These extinctions likely reduced the population of large-seeded tree species dependent on large herbivores for dispersal, and consequently, the range size of large seeded trees decreased by approximately 26–31%[129]. 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 about 1.5% after the extinction of megafauna[129].

Habitat heterogeneity has also played an important role in the formation of Amazonian biodiversity. The Andean uplift, with an average elevation of 4,000 m, created both habitat and climate heterogeneity while leading to the humidification of Amazonian lowlands and the aridification of Patagonia[130,131]. This has provided numerous opportunities for colonization, adaptation, and speciation events in a plethora of taxa, including frogs, birds, and plants, at different times[59,104,132,133]. As a consequence, the Andes are disproportionately highly biodiverse relative to their surface area[134]. 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[68,74,90].

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. Organismal behaviors strongly affect and even create many important habitats in the Amazon. Earthworms (Clitellata, Annelida) represent a classic example of how niche construction increases 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[135]. Several other Amazonian taxa are also

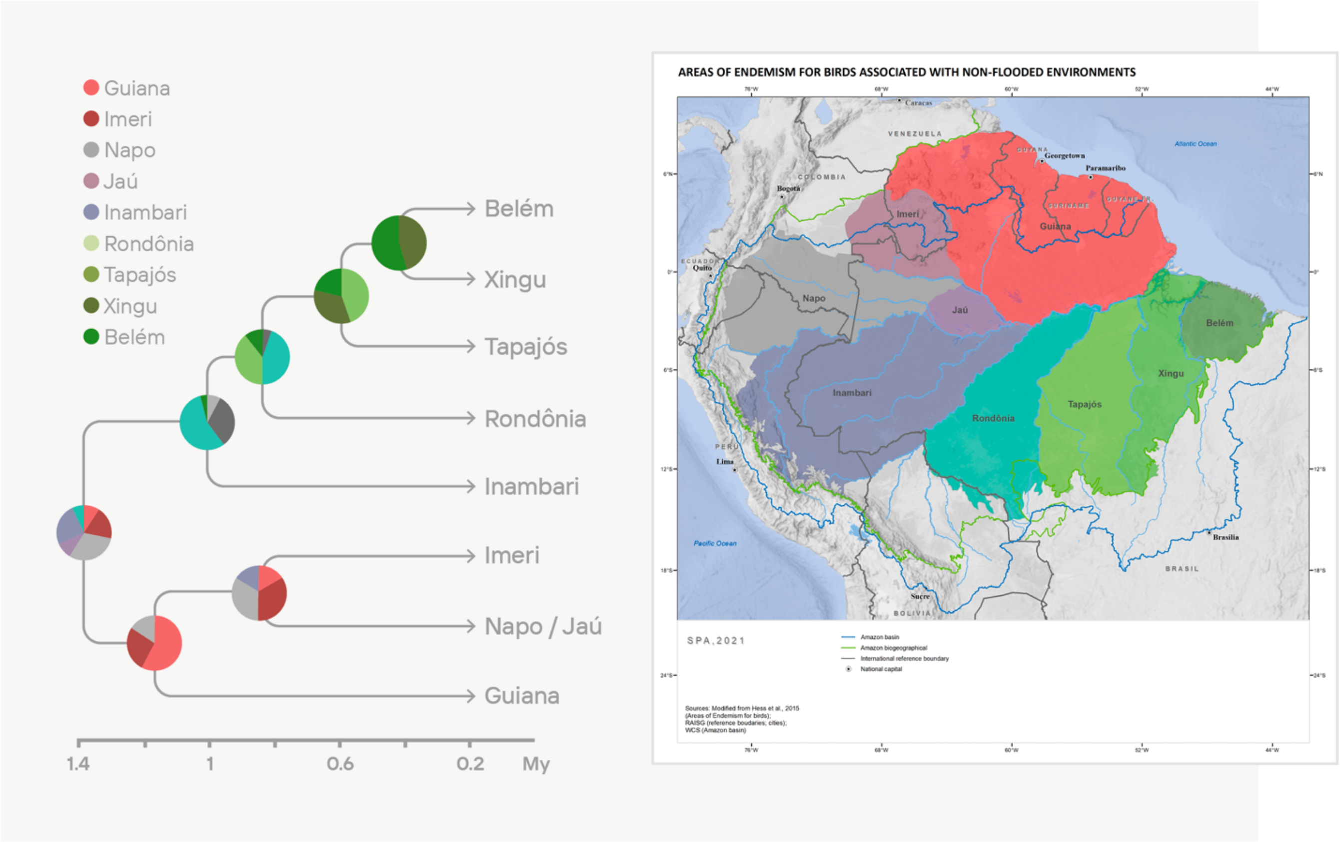

Figure 2.2 Summary of diversification patterns for 21 taxonomic clades of Amazonian birds restricted to the upland forest (*terra firme*) understory. Left: Relationships among nine areas of endemism, inferred from genetic data; pie charts denote ancestral area probabilities. Right: Areas of endemism currently recognized for upland forest birds[120, 121, 122].

important engineers of terrestrial ecosystems, including fungi[136], termites[137], and ants[138].

Adaptation to specific habitats has contributed significantly to species diversification in this region. For example, the large geographical extent of the Amazon, tied to its diverse soil types, provided multiple opportunities for ecological specialization[139,140]. The 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[141,142]). 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[112,124,143,144], with historically larger and more connected populations in the Western Amazon[144,145].

Conclusions The singular diversity of Amazonian organisms was generated over a period of millions of years and represents a large portion of Earth's known and unknown diversity. Because the Amazon has both current and historical connections with many other Neotropical biomes, forest destruction and species loss have direct impacts at both local and regional scales. Current declines in Amazonian biodiversity threaten the evolutionary process governing the origin and maintenance of species diversity in all of these areas. 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 heterogenous area. 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, areas holding distinct, unique, and/or higher amounts of evolutionary lineages should be given higher conservation priority. By prioritizing regions that host high genetic diversity, higher levels of phylogenetic uniqueness, and a broader spectrum of the genealogy of life, scientists can maximize future options, both for the continuing evolution of life on Earth and for their benefit to society. Maximum levels of global phylogenetic diversity led to higher ecosystem services globally and higher plant services in general for humankind.

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