Chapter 3 In Brief

Biological diversity and ecological networks in the Amazon

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THE AMAZON WE WANT
Science Panel for the Amazon

Biological diversity and ecological networks in the Amazon

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Key Messages & Recommendations

1) The Amazon basin is one of the most biodiverse areas in the world for most taxonomic groups. However, diversity varies geographically, with some groups being more diverse in the Amazon lowlands, whereas others thrive in the Andes.
2) Current evaluations underestimate the true species richness of the Amazon, partially due to the difficulty of sampling in this vast region. The Amazon presents an incredibly high rate of discovery of new species (one every other day) and, at the current rate, it will take several hundred years to compile a complete list of plants and animals (not to mention their geographic distribution, natural history, and conservation status). Further, some groups, such as fungi and bacteria, are understudied.
3) Plant-animal interactions are a central ecological process in Amazonian forests, without which these forests would cease to exist. Such interactions have led to the evolution of high species diversity. These networks of mutualists and consumers determine all aspects of Amazonian forests and are responsible for their composition, species regulation, recovery from disturbance, and the generation of biodiversity that comprises the forest.
4) It is essential to halt deforestation and forest fragmentation, and to establish large-scale, landscape-level restoration and conservation initiatives that maintain core areas (including terrestrial and aquatic environments, which are interdependent) and connectivity between areas. This is essential to securing the survival of species with large ranges, migration patterns,

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patchy distributions, and/or low population numbers, and the diversity of functional traits they present.

Abstract This chapter provides an overview of biodiversity in the Amazon, discusses the reasons why this region is so rich in species and ecosystems, and outlines some outstanding ecological processes that make the Amazon an icon of the natural world. Featured terrestrial and aquatic taxonomic groups illustrate how much we know about diversity in the Amazon, and more importantly, how much we still do not know. A clear understanding of biodiversity levels and their spatial and temporal variations is crucial to understanding future stability under different climate change, land use change, forest fragmentation, and deforestation scenarios and informing conservation and restoration efforts.

Why is the Amazon so rich in species and ecosystems? The Amazon is the most biologically diverse area on the planet. Encompassing around 7 million km^2, its biodiversity is incommensurable. More than one tenth of the world's species occur in this region[1,2]. It is estimated for the Amazon basin a richness of 50,000 vascular plants and 2,406 fish[3,4]; in the rainforest there are an estimated 427 amphibians, 371 reptiles, 1,300 birds and 425 mammals[5]. These numbers are gross underestimates, and in many cases biased towards the Brazilian Amazon. Many processes contributed to the evolution of such high biodiversity. Geological, hydro-climatic, evolutionary, and ecological factors are important, as well as disturbance regimes (see Chapters 1 and 2) and the cultural landscape (see Chapters 8-13). The relationship between biological, climatic, and geological data[6] is important in understanding the environmental history, origin, and fate of Amazonian biodiversity. However, biogeographic patterns vary considerably among taxonomic groups, adding complexity to the analysis[7]. A fundamental driver of regional biological diversity is the environmental heterogeneity associated with the rise of the Andes, the fluctuation of seasonal floods in the great alluvial plains, and macro-regional climatic events[8] (Figure 3.1).

Biological diversity patterns of selected taxonomic groups

Vascular plants The Amazonian countries are known to harbor some 79,600 species of native vascular plants, or 20% of all of the world's plant species[9–11]. There is no authoritative list of all vascular plants of the Amazon basin, but estimates for seed plants occurring below 1,000 m vary from 14,000 to 50,000 species[12–14]. Estimates for lowland trees vary between 6,727 to 16,000 species, including at least 1,000 flood-resistant trees and 388 herbaceous plants[14–18]. With such imperfect knowledge of Amazonian plants richness, unknown species could go extinct without even being described[19]. Endemic plant species from Ecuador, Peru, and Brazil (13,165 species) represent about 19% of the total endemic species (ca. 67,900) from tropical South America[9].

Fungi, algae, and non-vascular plants Traditionally called cryptogams, non-vascular plants include bryophytes, algae, lichens, and fungi, and they are the main drivers of the carbon and nutrient cycle and hydrology at high latitudes[20–22]. Biogeographically, non-vascular plants have their center of diversity in the Tropical Andes, and their species diversity is positively correlated to altitude.

Often overlooked in these habitats, the total diversity of these taxa is typically underestimated[23]. The estimated number of algae is believed to be between 30,000 and 50,000, of which only half have been described[24]. Recent studies have suggested that fungal diversity is greater in the tropics than in subtropical mountainous areas[25,26], although these areas have been studied considerably less[27]. Amazonian lichens number an estimated 150-200 species[28–31]. Finally, mosses are the dominant vegetation cover in a wide range of ecosystems, but their diversity in the Amazon is relatively low. Although 40 to 50 species can be found in any particular site, the increase in additional species from one site to another is low[32].

Insects Amazonian entomofauna is amazingly rich along the different vertical forest strata, and

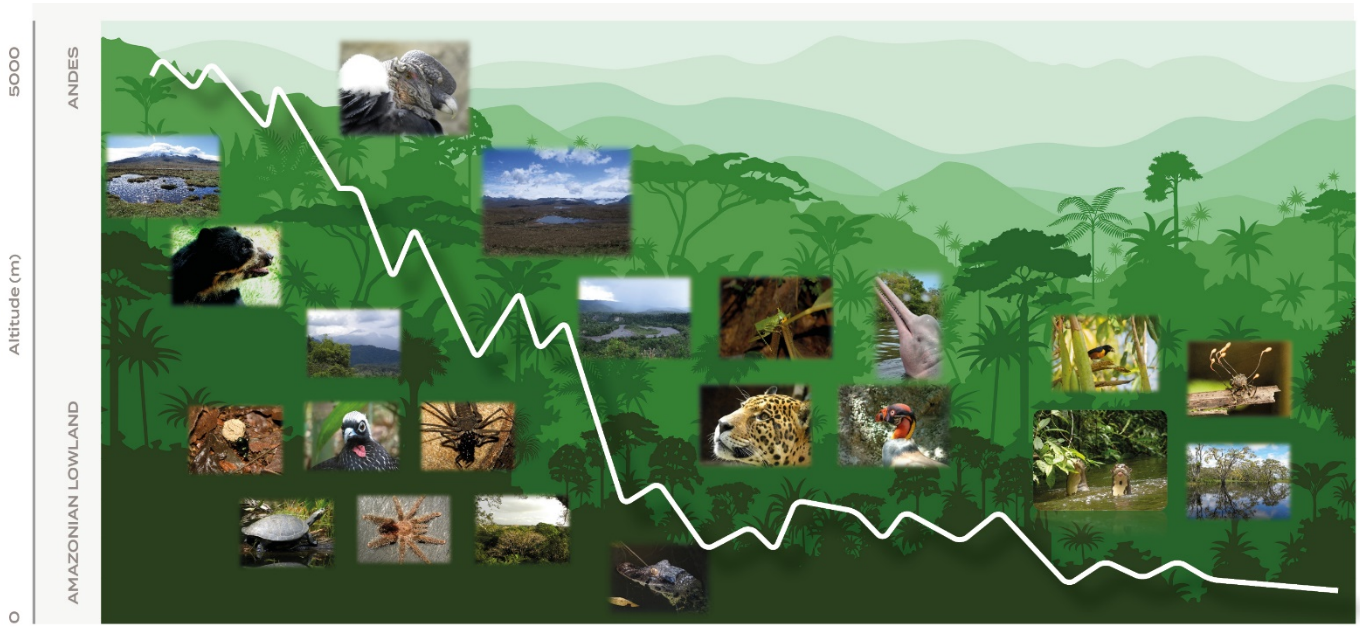

Figure 3.1 The Amazon is the most biodiverse area for most taxonomic groups. Photos show iconic species and ecosystems along the altitudinal gradient of the region, and selected species interactions. Background illustration by ekolara. Photos by Esteban Suaréz, Galo Zapata-Ríos, Fernando Trujillo, Robert Schlappal/©Superbass / CC-BY-SA-3.0 (via Wikimedia Commons).

patterns of species distribution at large spatial scales are not even across the region[33,34]. Insects inhabiting the forest canopy exhibit high numbers of species and high population densities[35,36]. For example, ants and mosquitoes (Formicidae and Diptera) represent 52% and 10%, respectively, of the more than 300 arthropods found per square meter. In addition, in one study 95 different ant species were found on a single tree, as many as found in the entirety of Germany[37]. There is limited information about the centers of evolution and dispersal of Amazonian insects and other arthropods. High diversity of aquatic insects is associated with the environmental heterogeneity of the ecosystems they inhabit. Species from ten insect orders have specialized aquatic or semi-aquatic habits. The order Diptera stands out, representing half of known aquatic insects, notably Chironomidae[38]. The maintenance of riparian forests and associated aquatic environments is crucial to prevent the loss of species and ecosystem services provided by aquatic insect communities[39,40].

Fish The Amazon basin contains the world's most diverse strictly-freshwater fish, with 2,406 species belonging to 514 genera, 56 families, and 18 orders[4]. This exceptional diversity, which represents approximately 15% of the world's freshwater fishes, includes 58% of species found nowhere else on Earth (1,402 endemic species[4]). This includes marine taxa that have adapted to freshwater, such as Amazonian stingrays. Amazonian fishes come in a large array of sizes, from miniature species under 20 mm[41] to those that reach 3 m or more in length, such as the pirarucu (paiche, *Arapaima gigas*) or the goliath catfish (*Brachyplatystoma filamentosum)*, both weighing more than 200 kg[42,43]. Unlike many other river basins, where species richness increases as you move downstream[44,45], Amazonian species show decreasing West-East gradients, suggesting that contemporary fauna originated in the western portion of the basin[46]. This pattern also indicates that colonization of the eastern portion of the basin is still incomplete, consistent with the relatively recent establishment of the modern Amazon River about 2.5 million years ago.

Figure 3.2 Amphibian diversity in the Amazon basin. (A) Embryos of the Andean glassfrog *Nymphargus wileyi*. (B) Torrent frog, *Hyloscirtus staufferorum*. (C) Tiger-stripeed Monkey Frog, *Callimedusa tomopterna*. (D) Amazonian salamander, *Bolitoglossa* sp. Photos by Tropical Herping.

Amphibians and reptiles Of the more than 8,300 species of amphibians known to exist today[47], the Amazon basin exhibits the highest density and the highest number of endangered species[48–50]. Amphibian biodiversity patterns display considerable variation within the Amazon basin (Figure 3.2), often driven by topography, hydrology, evolutionary history, and ecology[51]. Amphibian groups such as the tree frogs, monkey frogs, and poison-arrow frogs are more diverse in the lowland rainforests, whereas others, such as glass frogs, harlequin toads, and marsupial frogs, are more diverse in the Andean cloud forests[47,52].

The Amazon basin has a high diversity of reptile species, approximately 371, occupying a large variety of terrestrial and aquatic environments[2,53]. Patterns of diversity and distribution of reptiles indicate that species richness usually decreases with latitude and from west to east[54–56]. Studies carried out in the northwestern Amazon indicate a greater diversity of squamate reptiles relative to the southeastern Amazonian plain[54,57]. Although most species of reptiles are considered terrestrial, at least 40 use the aquatic environment and depend upon it for their survival, including four species of crocodilians, two lizards, 16 turtles, and many snakes[58,59].

Birds The Amazon hosts the highest number of bird species in the world, with more than 1,000 species, of which about 265 are endemic[60,61]. The true number of species could be much higher, as several genetically-divergent lineages may represent new cryptic species[62]. Bird diversity increases with proximity to the Andes. Topography and ecology change at an elevation of approximately 500 m, where many lowland bird species (~800) reach their upper elevational range, and many Andean reach their lowest elevational range[61,63]. The wetter western Amazon is home to older, richer bird species when compared to the dryer eastern Amazon[64].

Mammals The Amazonian region harbors one of the richest mammalian faunas of the world, with approximately 140 genera and 425 species. Amazonian mammals account for approximately one-third of all South American mammalian diversity, or about 1,260 species[65]. However, the number of mammal species at any single locality in Amazonia varies greatly depending on forest type and habitat diversity. Mammal communities in seasonally flooded (*várzea*) forests can be considered relatively impoverished when compared with neighboring *terra firme* forests, although density and biomass can be significantly higher in *várzea* than in *terra firme*[66,67]. Endemism is also very high, with 10 endemic genera and 144 species (34%) found only in the Amazon[68,69]. This impressive diversity is not distributed equally among orders; marsupials, rodents, and primates together comprise approximately 80% percent of all endemic species[70,71]. It has been suggested that mammalian communities in the western Amazon are the most diverse in the region, the Neotropics, and probably the world[71–73].

Parasites and pathogens Despite accounting for one-third to over half of the species on Earth[74], parasites and pathogens are usually ignored by biodiversity inventories and conservation studies[75]. For example, of the c. 430 wild mammal species that occur in the region, only 185 have been studied with regards to their interactions with parasites. The parasite groups with the highest number of species reported interacting with wild mammals are helminths (77), arthropod ectoparasites (65), viruses (62), protozoans (29), bacteria (12), and fungi (7). From those, 38 viruses, 16 arboviruses, 11 bacteria, nine helminths, 19 protozoans, one ectoparasite, and seven fungi are known to be zoonotic and cause diseases in humans. Concerning the arthropod-borne viruses (arboviruses), 27 different species have already been recorded infecting wild mammals in the Amazon region. From those, 16 species are known to be zoonotic, including Caraparu, Changuinola, dengue, Guama, Mayaro, Marituba, Murutucu, Oriboca, Oropouche, Piry, Saint Louis, Tacaiuma, and yellow fever, often shared with domesticated mammals such as pets and cattle.

Outstanding ecological processes and adaptations in terrestrial and aquatic ecosystems

Plant-animal interactions Plant-animal interactions are a central ecological process in Amazonian forests, without which these forests would cease to exist. Of the trees in the Amazonian forest ecosystem, 80-90% rely on animals for seed dispersal[76,77] (Figure 3.3), and as many as 98% of plant species rely on animals for pollination[78]. Animals are coopted into dispersal by a wide variety of plant strategies; birds, mammals, fish, and insects respond to different plant strategies[79].

Vast areas of the Amazon are seasonally flooded, and fish have been shown to be critical seed dispersers in these forests[80,81] (see Chapter 4). Many migratory fishes have co-evolved a mutually beneficial relationship with the forest. During the high-water season, migratory fishes invade the flooded forest to feed on fruit, dispersing seeds over large distances and improving their chances of germination[81–83].

Figure 3.3 Seed dispersal by Rufous-bellied Euphonia (*Euphonia rufiventris*). Photo: Esteban Suárez.

Most of the roughly 150 known frugivorous fish species found in the Neotropics also occur in the Amazon basin[84], where they consume at least 566 species of fruits and seeds[81]. Pollination networks in Amazonian forests are highly diverse, complex, and include a wide variety of invertebrates and vertebrates[78,85]. Pollinator networks are often highly specialized, underscoring the role of pollinator conservation in preserving overall Amazonian biodiversity and ecosystem services[86,87]. Consumptive effects[i] generate diversity through coevolutionary arms-races and control plant and animal biodiversity on ecological and evolutionary time scales.

[i]Effect of predator in consuming pray by altering the likelihood of local prey extinction[126].

Plant-herbivore interactions have led to the evolution of high species diversity by locking groups of organisms in evolutionary arms races of attack and defense (e.g., production of secondary compounds in trees of *Protium subserratum*)[88,89], leading to a spectacular diversification in Amazonian chemical defenses[90,91]. Networks of mutualists and consumers determine all aspects of Amazonian forests, and are responsible for their composition, species regulation, and recovery from disturbance. Changes in species interactions can have cascading and long-term consequences for ecosystems[92].

Floods and adaptation of organisms Aquatic ecosystems are a complex mosaic of habitats influenced by floods[ii] (see Chapter 4) and nutrient flows. This has generated areas with high and low productivity and promoted complex adaptation processes. Many species have special adaptations to withstand low oxygen levels and high temperatures during periods of drought[93–97]. Other species, including many fishes, choose to migrate between main channels, lakes, and small tributaries, particularly the Prochilodontidae and Curimatidae families. Species such as the pirarucu (paiche, *Arapaima gigas*) build nests at the bottom of lakes and reproduce during the low water season. When the water level rises, they make small lateral migrations towards the flooded forest, where the males care for their young. In response to fish migrations, some aquatic carnivores have evolved to catch fish hidden among vegetation. For example, the Amazon River dolphin's (*Inia geoffrensis*) unfused cervical vertebrae, long snout, and short dorsal and pectoral fins allow them to navigate and catch fish among submerged vegetation. Giant otters (*Pteronura brasiliensis*) have more or less well-defined territories during the low water period, but increase their territories in the wet season to include flooded forest areas. Jaguars (*Panthera onca*) can spend up to three months living in the treetops above floodwaters, feeding especially on sloths, alligators, and giant otters[98,99].

The flood cycle has also generated exceptional adaptation processes in plants, such as those which can survive being submerged for several months (e.g., *Nectandra amazonum, Symmeria paniculata*) and those which synchronize fruiting to coincide with floods and the return of frugivorous fishes. Likewise, during floods the proliferation of aquatic vegetation provides food for other species, such as manatees and capybaras[100–102].

Fish migrations and floodplain nutrient flow Migratory fishes play important roles in aquatic food webs, providing crucial exchanges between different components of ecosystems. Amazonian goliath catfish of the genus *Brachyplatystoma* perform the longest known freshwater migrations. One species, *B. rousseauxii*, uses almost the entire length of the Amazon basin in a round trip migration of up to 12,000 km between its spawning grounds in the Andes and its nursery in the estuary[103–107]. This exceptional migration involves natal homing, a behavior seldom observed in freshwater species, but common in species migrating between rivers and the sea, such as salmon. In this process adult fish usually return to the watershed where they were born, either in the upper Madeira[104] or Amazon[107]. These extraordinary apex predators[103] are under threat from overharvesting[108–111].

Fish migrations, and in particular the movements of detritivorous fish, play crucial roles in nutrient transport important for local food webs. Fishes of the family Prochilodontidae (*Prochilodus* and *Semaprochilodus*), undertake complex, large-scale migrations from rich white water floodplains where they reproduce and feed[112–114] to nutrient-poor tributaries (black or clear waters) where they sustain local predatory fish species[115,116]. Some detritivorous fish also modulate nutrient cycling in Amazonian streams[117,118], and their decline due to overfishing and disruption by dams can have profound consequences nitrogen and phosphorus flows[119].

[ii]The annual inundation and drought cycle of Amazonian floodplains is the principal driving force responsible for the existence, productivity, and interactions of the major biota in a river-floodplain system (Chapter 4).

Functional diversity Functional diversity is understood as the value, range, and distribution of functional traits in a given community[120,121]. The Amazon is among the most functionally diverse regions on Earth for several taxa (e.g., fish[122], plants[123], amphibians[124]). Taxonomic and functional diversity are often decoupled, and for some taxonomic groups, functional diversity is considerably higher in the Amazon than what would be expected based on their taxonomic diversity. The Neotropics host approximately 40% of the world's freshwater fish species, yet this same region hosts more than 75% of fish functional diversity. Fish functional diversity in the Amazon includes incredible variation in body form and trophic ecology, ranging from catfish with specialized teeth and jawbones for consuming submerged tree trunks (e.g., Cochliodon, Panaque spp), to electric fish with reduced eyes living in turbid waters (Gymnotiformes), to migratory frugivores with molar-like teeth that are important seed dispersal agents (e.g., Colossoma, Piaractus[81]), to elongated vampire catfishes that feed on blood in the gills of other fishes (Vandellia)[125]. Functional diversity contributes to community and ecosystem resilience to climate change, deforestation, or other disruptions. Models suggest that forests with high plant trait diversity will regenerate more rapidly than forests with low plant trait diversity following the loss of large trees due to climate change (see Chapter 23).

Conclusions While the Amazon is one of the largest and most intact ecosystems in the world, it is also one of the least known biologically. Its immense size, diversity, and remoteness make the task of documenting its biodiversity extremely challenging. Consequently, there are both spatial and taxonomic biases in existing data. This, combined with our general lack of adequate data overall, affects our capacity to understand the true patterns of biodiversity in the Amazon. This includes questions such as precisely where centers of endemism are located and where one might find the most endangered species - matters of great concern for conservation. Nevertheless, while such limitations are problematic, the reality is that all ecosystems have data gaps, and we must make decisions using the best information available, recognizing that as we learn more, it may be wise to improve upon past decisions.

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