Amazon Assessment Report 2021

Chapter 3

Biological diversity and ecological networks in the Amazon


Dentro da Reserva de Desenvolvimento Sustentável Vitória de Souzel 2018 (Foto: Lilo Clareto/Amazônia Real)

THE AMAZON WE WANT
Science Panel for the Amazon

SUSTAINABLE DEVELOPMENT SOLUTIONS NETWORK
A GLOBAL INITIATIVE FOR THE UNITED NATIONS

About the Science Panel for the Amazon (SPA)

The Science Panel for the Amazon is an unprecedented initiative convened under the auspices of the United Nations Sustainable Development Solutions Network (SDSN). The SPA is composed of over 200 preeminent scientists and researchers from the eight Amazonian countries, French Guiana, and global partners. These experts came together to debate, analyze, and assemble the accumulated knowledge of the scientific community, Indigenous peoples, and other stakeholders that live and work in the Amazon.

The Panel is inspired by the Leticia Pact for the Amazon. This is a first-of-its-kind Report which provides a comprehensive, objective, open, transparent, systematic, and rigorous scientific assessment of the state of the Amazon's ecosystems, current trends, and their implications for the long-term well-being of the region, as well as opportunities and policy relevant options for conservation and sustainable development.

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Graphical Abstract

- The Amazon basin is one of the most biodiverse areas for most taxonomic groups. However, knowledge of basin-wide richness patterns remains incomplete and its true richness underestimated.

- Diversity varies geographically, with some groups being more diverse in the Amazon lowlands, whereas others thrive in the Andes.

- Plant-animal and trophic interactions are central ecological processes in Amazonian forests, without which these forests would cease to exist.

- Maintaining altitudinal connectivity from the Amazon to the Andes is crucial to conserve Amazon basin biodiversity.

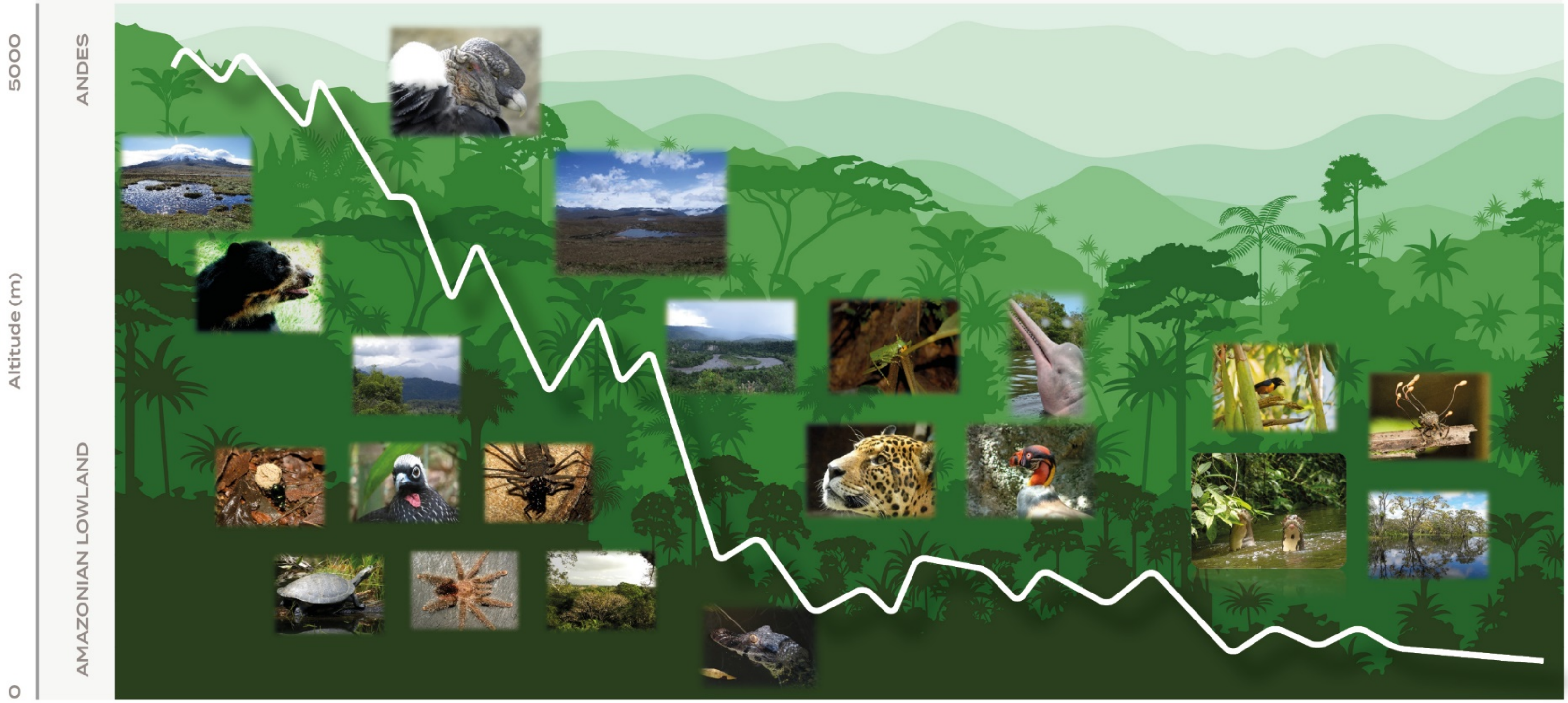

Figure 3.A The Amazon is the most biodiverse area for most taxonomic groups. Photos show iconic species and ecosystems along the altitudinal gradient of the region, as well as selected species interactions. Background illustration by ekolara. Photos by Esteban Suaréz, Galo Zapata-Ríos, Fernando Trujillo, Robert Schlappal/© Superbass / CC-BY-SA-3.0 (via Wikimedia Commons).

Biological Diversity and Ecological Networks in the Amazon

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Key Messages

- The Amazon Basin is one of the most biodiverse areas in the world for most taxonomic groups. Diversity varies geographically, with some groups being more diverse in the Amazonian lowlands, whereas others thrive in the Andes.
- Current evaluations underestimate the true species richness of the Amazon, partially because of the difficulty of sampling in this vast region. The Amazon exhibits an incredibly high rate of discovery of new species (one every second 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). Furthermore, some groups, such as fungi, algae, lichens, and bacteria, are understudied.
- 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 the biodiversity that comprises the forest, rivers, and other ecosystems.

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Abstract

Scientists have not been able to estimate, to the nearest order of magnitude, the number of species in the Amazon. Although the Amazon includes one of the largest forests in the world, it is also one of the least known biologically. Documenting its biodiversity is challenging because of its immense size, heterogeneity, and limited access. Based on current knowledge, the Amazon exhibits the highest density of species as well as the highest number of threatened species (many of them endemic) for vascular and non-vascular plants, fish, amphibians, birds, and mammals. Deeper knowledge of biodiversity patterns is still lacking, and the spatial turnover of species assemblages at different scales remains poorly understood. In the Amazon, we can also find some outstanding examples of animal behavior. For example, many fish migrate over long distances, and some of them perform the longest known freshwater migrations in the world, traveling the entire length of the Amazon Basin in a round trip migration of~12,000 km. It is also important to consider that plant-animal interactions and trophic interactions are central ecological processes in Amazonian forests. Disruptions of these interactions can alter forest community composition over the long-term. Functional diversity, including intra- and inter-specific variation, has recently attracted the attention of scientists, and it is evident that it contributes to community and ecosystem resilience to perturbations, including climate change. There is still much to learn about Amazonian biodiversity, species assemblages, and ecological interactions. There are spatial and taxonomic biases in the data (including many unexplored locations and lesser-known taxonomic groups), which affect our understanding of biodiversity patterns in the Amazon. This chapter highlights the need for more basic and applied research to improve our knowledge of biodiversity patterns across the region. This information is critical for understanding the impacts of human activities and informing conservation and restoration actions.

Keywords: Biodiversity, species richness, endemism, fauna, flora, fauna, plant-animal interactions, migration, phylogenetic diversity, functional diversity.

3.1 Why is the Amazon so rich in species and ecosystems?

The Amazon is the most biologically diverse area on the planet. Encompassing approximately 5,800,000 km^2, the biodiversity in the Amazon biogeographic province is incommensurable. More than one tenth of the world's species occur in this region (Mittermeier *et al.* 2002). Assessments of species richness indicate close to 50,000 vascular plants, at least 2,406 fishes in the Amazon Basin, and 427 amphibians, 371 reptiles, 1,300 birds, and 425 mammals in the Amazon rainforest (Mittermeier et al, 2003, Hubell *et al.* 2008, Jézéquel *et al.* 2020). These numbers are gross underestimations of the real numbers, and for some groups are biased to the Brazilian Amazon (http://censo.museugoeldi.br:8080/museugoeldi-web-1.2.0). In addition, these numbers highlight the need for more basic research on biodiversity patterns throughout the region (see Box 3.2 for estimates of species richness numbers that include the Andean section of the Basin, based on records from the Global Biodiversity Information Facility, GBIF). Endemism is also high in the Amazon Basin. For example, in the Amazonian lowlands approximately 40% of mammals, 70% of reptiles, and 86% of amphibians are not found elsewhere (Mittermeier *et al.* 2003). Amazonian ecosystems range from forests and savannas to wetlands (see Chapter 4). The three main types of water (white-, black-, and clear-waters) differ in their origin and composition of sediments and minerals, forming a unique mosaic of freshwater ecosystems throughout the Basin (see Chapter 4). The diversity of life in the Amazon is astonishing, but why is the Amazon so rich in species and ecosystems? Many processes have contributed to generate the high Amazonian biodiversity (see Chapter 2 for different models of diversification). Variables including tectonics, hydroclimate, evolutionary and ecological factors (see Chapter 2), disturbance regimes, and the more recent legacy of a cultural landscape (see Chapter 10) are among the most important processes.

Biodiversity refers to the number of species, the variety, and variability of living organisms (*e.g.*, plants, animals, fungi, microorganisms), including terrestrial, subterranean, marine, and other aquatic ecosystems, and the ecological complexes of which they are a part. Included in the concept of biodiversity is the variety within species (genetic diversity), between species, and of ecosystems (UN Convention on Biological Diversity, https://www.cbd.int/convention/articles/?a =cbd-02). Scientists have not yet estimated to the nearest order of magnitude the number of species living in the Amazon. Researchers continue to discover new species, even among the best-known taxonomic groups, such as mammals and birds (Patterson 2001, Milá *et al.* 2012, Ribas and Aleixo 2019). For many invertebrate taxa, undescribed biodiversity is so prevalent that scientists have described only a small fraction of the species that occur in the region.

The Amazon is a global icon of biodiversity. Current knowledge on the distribution of species suggests complex biogeographic patterns (Ribas *et al.* 2012, Naka and Brumfield 2018, Silva *et al.* 2019, Moraes *et al.* 2020). After considering these biogeographic patterns and the geological and climatic history of the region, researchers have proposed several hypotheses to explain the origin of high Amazonian biodiversity (Haffer 2008, Leite and Rogers 2013). The relationship between biological, climate, and geological data (Baker *et al.* 2014) is important to elucidate the environmental history, origin, and fate of Amazonian biodiversity. However, biogeographic patterns vary considerably among taxonomic grou-ps, adding complexity to the analysis of environmental history and biotic diversification.

The establishment of a transcontinental drainage system during the Miocene (9.4 to 9.0 Ma) may have promoted the recent evolution of *terra firme* communities in the lowlands of the western Amazon (Hoorn *et al.* 2010, Ribas and Aleixo 2019). In contrast, the different flooded habitats depend on the environments associated with river dynamics and the cycle of floods (the flood pulse), so their evolution is linked to the broad Amazon drainage system (Toews *et al.* 2016, Moraes *et al.* 2016). Riverine dynamics could have influenced the recent evolution and distribution of species adapted to flooded environments and possibly interrupted movement between eastern and western populations of the Amazon, as suggested by phenotypic variation in vertebrates and confirmed by genomic analyses (e.g., Leite and Rogers 2013). In addition, as a response to broader geological changes, most species were able to generate different degrees of intraspecific genetic diversity, depending on how they responded to physical changes in their habitats (Ribas and Aleixo 2019). Therefore, another fundamental driver for regional biological diversity is the environmental heterogeneity associated with the rise of the Andes, and the pulse and fluctuation of seasonal floods in the great alluvial river plains of the Amazon, complemented by macro-regional climatic events (Junk 1997).

This chapter provides an overview of biodiversity in the Amazon region, explains 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. Selected terrestrial and aquatic taxonomic grou-ps exhibit how much we know and more importantly how much we still do not know and have to discover. A clear understanding of biodiversity levels and their spatial and temporal variations is crucial to understanding future stability under different climate-change scenarios, and informing conservation efforts.

3.2 Biological diversity patterns of selected taxonomic groups

3.2.1 Vascular Plants

Intangible oral transmission perpetuated traditional knowledge, agricultural practices, medicinal uses, and culinary uses of Amazonian plants from generation to generation. Pictorial depictions in artifacts (e.g., textiles, pottery, jewelry) and archeological remnants left across the land (see for example Mesía Montenegro 2014, Zarillo *et al.* 2018) point to traditional uses and domestication of many plants (Box 3.1). The first Europe-ans chronicled and illustrated domesticated plants, such as chili pepper, cassava, and tobacco, as well as the first illustration and delicious description of the pineapple (Cobo 1964[1653], Fernández de Oviedo and Valdés 1526, Myers 2007, Piso and Marcgrave

1648). Despite the long traditional use of some of these plants, the potential benefits of the vast majority of species are still unknown (Alcantara-Rodriguez 2019, Antonelli *et al.* 2019, National Research Council 1989). The Spanish crown financed botanical expeditions to the South American colonies in the eighteenth century with the goal of discovering and documenting medicinal plants, such as quinine (cascarilla bark, *Cinchona officinalis*; Ruiz 1792, Ruiz and Pavón 1801). These early expeditions, along with later European ones, collected thousands of herbarium specimens and published works that built the foundation of modern Amazonian plant taxonomy (e.g., Aublet 1775, French Guiana; Ruiz and Pavón 1798–1802, Peru; Humboldt and Bonpland 1816–1818, northern South America; von Martius and collaborators 1840–1906, Brazil, at the time the first complete flora of a South American country). In the nineteenth century, the first museums and associated herbaria opened in the nascent republics (National Museum in Rio de Janeiro in 1831, Quito Central University in 1860, Museu Paraénse Emílio Goeldi in 1866, Georgetown University in 1879, Rio de Janeiro Botanical Garden in 1890), followed by many others at the turn of the twentieth century. During the second half of the twentieth century, numerous in-country initiatives and international collaborations in botanical research and exploration resulted in new herbaria in museums and universities, thousands of specimens collected, new species of plants described for science, and an array of floristic research publications. In the last thirty years, with the advancement of electronic resources (virtual herbaria, digital libraries, databases) plant catalogues or checklists (a curated list of species names) became a faster way to compile information and have been published for each country (BFG 2018, Ulloa Ulloa *et al.* 2017, Ulloa Ulloa and Jørgensen 2018, Table 3.1). There is still no complete modern flora (in the form of revisionary descriptive work, with identifications keys, and illustrations) for any country in the region, but innovative online collaborations are underway (Table 3.1). A recent compilation of a list of vascular plants of the Americas (Ulloa Ulloa *et al.* 2017) synthesized the remarkable achievements of plant expeditions, collectors, and describers, regional floras, and tens of thousands of publications (Givnish, 2017). The Amazonian countries (Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, Guyana, Suriname, and the French overseas department of French Guiana) are known to harbor some 79,600 species of native vascular plants, which correspond to 20% of all of the world's plants (Ulloa Ulloa *et al.* 2017, 2020; Nic Lughadha *et al.* 2016; Table 3.1). Approximately 4% of the plant species descriptions were added from 2017 to 2020, and of the 79,600 vascular plants currently known, 61% (48,531) are endemic (Ulloa Ulloa *et al.* 2020, Table 3.1, Figure 3.1). There is no authoritative list of all of vascular plants of the Amazon Basin, but estimates for seed plants occurring below 1,000 m vary from 14,000 to 50,000 species (Gentry *et al.* 1997, Lewinsohn and Prado 2005, Cardoso *et al.* 2017). Estimates for lowland trees varies between 6,000 and 16,000 species, including at least 1,000 flood-resistant trees and 388 herbaceous plants (Junk and Piedade 1993; Cardoso *et al.* 2017; ter Steege *et al.* 2016, 2020), emphasizing our imperfect knowledge of the richness for Amazonian plants.

Human activities may threaten many Amazonian plant species, particularly those with restricted geographical ranges (Ulloa Ulloa *et al.* 2017). The IUCN (International Union for Conservation of Nature, 2001) Red List categories were used to assess the conservation status of endemic plants of Ecuador (León-Yánez *et al.* 2011), Peru (León *et al.* 2006), and Brazil (Martins *et al.* 2018). Sixty-five percent of the endemic species evaluated (8,564) are threatened, i.e., listed as Critically Endangered (CR), Endangered (EN), or Vulnerable (VU) in the IUCN Red List of Threatened Species (Figure 3.2). This percentage is well above the world wide estimated risk for tropical countries of 47% (Pitman and Jørgensen 2002). In addition, 2,011 endemic species were Data Deficient (i.e., without enough information for a detailed assessment), which could underestimate the number of threatened species. Poorly known species could become extinct without even being reported (Humphreys *et al.* 2019). The endemic plants evaluated from Ecuador, Peru, and Brazil (13,165 species) combined represent approximately 19% of all endemic species (*ca.* 67,900) from tropical South America (Ulloa Ulloa *et al.* 2017, Figure 3.2). For Ecuador alone, 78% of endemic plant species are under risk due to deforestation or habitat alteration (León-Yánez *et*

Table 3.1. Native vascular plant (all plants) diversity in Amazonian countries and references.

Country/Region	**Guianas (Guyana, Suriname, French Guiana)**	**Venezuela**	**Colombia**	**Ecuador**	**Peru**	**Bolivia**	**Brazil**
Total Vascular Plants (Numbers in parenthesis are total number of endemic species) **(Ulloa Ulloa *et al.* 2020)**	**8,389** (1,183)	**15,395** (3,475)	**24,047** (7,420)	**18,505** (5,992)	**19,836** (7,875)	**14,736** (3,097)	**34,472** (19,489)
Below 1000 m, Seed Plants (Cardoso *et al.* 2017 or specified)	**6,890** [incl. Venezuela]		**5,835** (Bernal *et al.* 2015)	**3,607**	**5,401**	**3,518**	**11,846** (BFG 2018)
Ongoing Country Flora	**Flora of the Guianas** (Görts-van Rijn and collaborators 1986–present)	**Flora de Venezuela** (Lasser *et al.* editors (1968–present) **Flora of the Venezuelan Guayana** (Steyermark *et al.* 1995–2005)	**Flora de Colombia** (1983–present)	**Flora of Ecuador** (Sparre *et al.* editors, 1973–present).	**Flora of Peru** (MacBride and collaborators 1936–present, see Gentry, 1980)	**Flora de Bolivia** (In preparation, see Menezes *et al.* 2015)	**Flora do Brasil 2020** online
Catalogue of Plants	**Funk *et al.* (2007); Feuillet (2009)**	**Hokche et *al.* (2008).**	**Bernal *et al.* (2015)**	**Jørgensen and León-Yánez (1999); Ulloa Ulloa and Neill (2005); Neill and Ulloa Ulloa (2011)**	**Brako and Zarucchi (1993); Ulloa Ulloa *et al.* (2004)**	**Jørgensen *et al.* (2014)**	**Forzza *et al.* (2010); BFG (2018)**
Red List Endemics		**Huérfano *et al.* (2020)**	Ongoing (**Calderón *et al.* 2002–present**, not exclusive to endemic plants)	**León-Yánez *et al.* 2011**	**León *et al.* (2006 [2007])**	Ongoing (**Navarro *et al.* 2012–present**)	**Martins *et al.* (2018)**
Useful / Medicinal Plants. There are numerous local and regional publications. Only country wide are cited here.		**Guánchez (1999)**	**Pérez Arbelaez (1956, 1990)**	**De La Torre *et al.* (2008); Ríos *et al.* (2007)**	**Brack Egg (1999), Reynel (2003).**		See **Dutra *et al.* (2016); Vieira *et al.* (2016); Coradin *et al.* (2018) Mors *et al.*, (2000), Modolo and Foglio (2019)**
Regional	**Correa Q. (1989); National Research Council (1989); Estrella (1995), Villachica (1996), Tejedor Garavito *et al.* (2012)**						

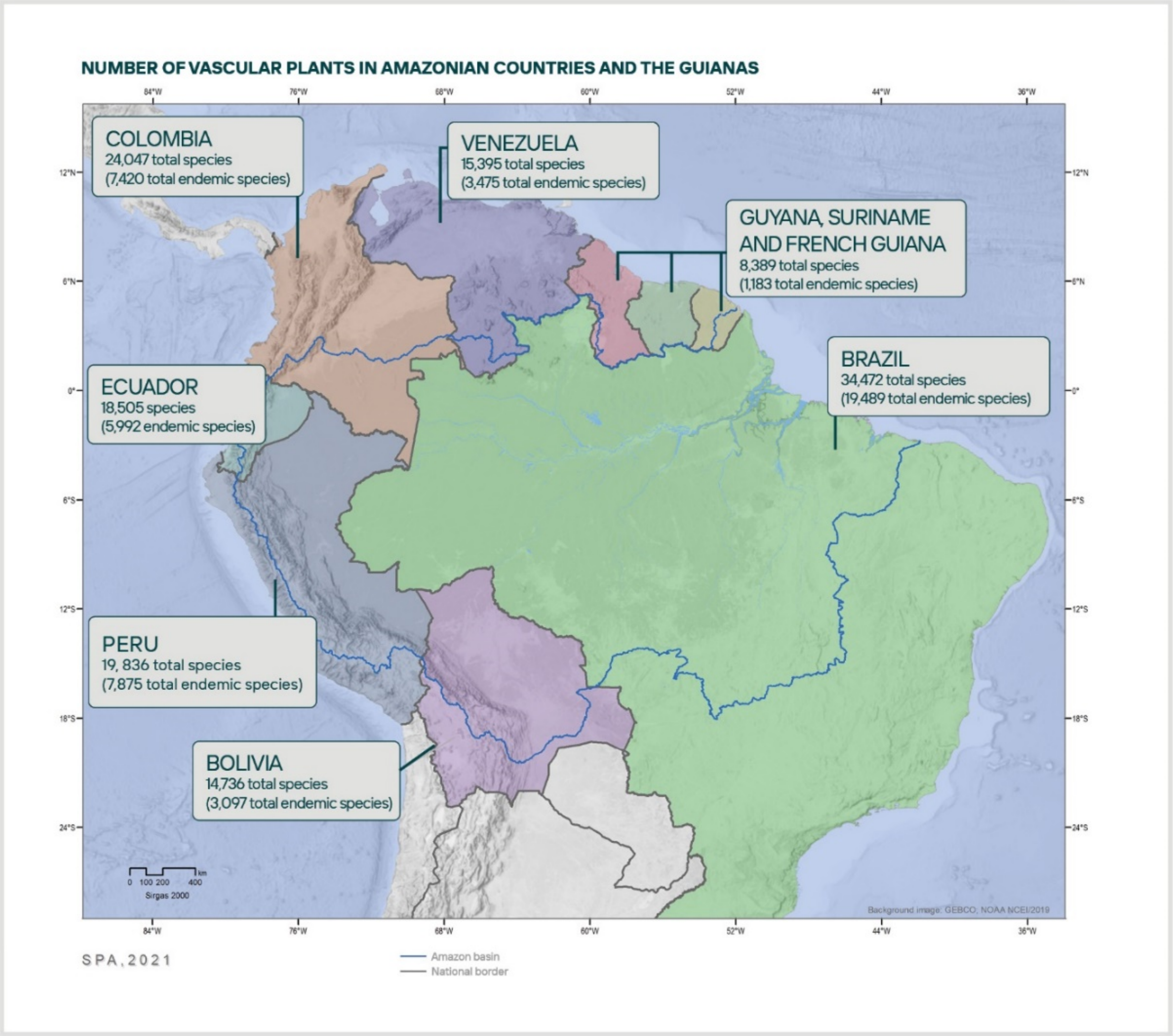


Figure 3.1 Number of vascular plants in Amazonian countries. For each area, the total number of species of native vascular plants and the number of endemic species (in parenthesis) are indicated (Data from Ulloa Ulloa *et al.* 2020. Illustration by C. Ulloa Ulloa).

al. 2011). Although national Red Lists and Red Data Books may be restricted geographically, they provide an overview of their status and a basis for conservation actions (Pitman and Jørgensen 2002).

3.2.2 Fungi, algae, and non-vascular plants

Non-vascular plants (liverworts, hornworts, mosses), algae, and fungi are the main drivers of the carbon and nutrient cycle at high altitude (Beringer *et al.* 2001, Lang *et al.* 2009). Biogeographically, the difference in the abundance of non-vascular plants in the Amazon is lower compared with Andean forests. As with vascular plants, non-vascular plants have their center of diversity in the tropical Andes, although there species diversity increase with altitude. Often overlooked in these habitats, the total diversity of these taxa is typically underestimated (Ferris *et al.* 1996).

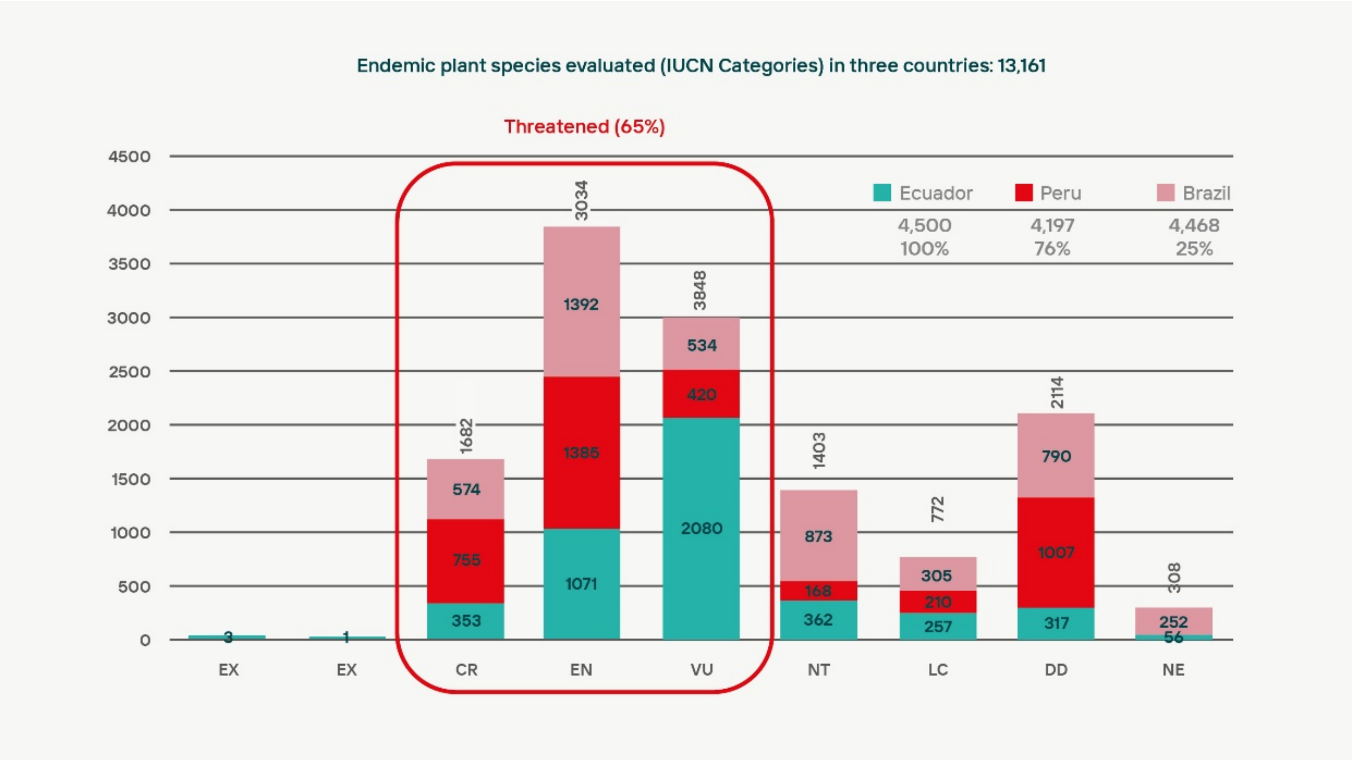


Figure 3.2 Plant endemics (all plants) of Brazil, Peru, and Ecuador evaluated with IUCN conservation status categories. The red rectangle encloses the three threatened IUCN Red List categories. IUCN categories: EX=Extinct; EW=Extinct in the Wild; CR=Critically Endangered; EN=Endangered; VU=Vulnerable; NT=Not Threatened; LC=Least Concern; DD=Data Deficient; NE=Not Evaluated. Number of endemic plant species evaluated: Ecuador 4,500 (100% of endemics, León-Yánez *et al.* 2011), Peru 4,197 (76%, León *et al.* 2007), Brazil 4,468 (25%, Martins *et al.* 2018).

There are a large number of species of algae and, although the bibliographic references significantly differ in the estimates of the number of species, it is believed that there are between 30,000 and 50,000 species, of which only half have been described (Dos Santos 2016). The information available on algae for the Amazon is very scarce; no research has attempted to characterize the flora of microalgae or subaerial algae of these forests and examine their biodiversity in detail using state-of-the-art methods (Lopez-Bautista *et al.* 2007). Presenting a synthesis of the biodiversity status of tropical forest algae is difficult or even impossible (Andersen, 1992).

Fungi, on the other hand, belong to their own kingdom, and are different organisms from plants and animals because they excrete digestive enzymes and absorb externally digested nutrients. Although the factors that determine their diversity remain little explored, estimates of the number of species on the planet vary from 500,000 to almost 10 million. Recent studies have suggested that fungal diversity is greater in the lowlands than in Andean slopes (Arnold and Lutzoni 2007; Tedersoo *et al.* 2014), but the later have been considerably less studied (Barnes *et al.* 2016). Lichens are composed of two organisms living symbiotically: fungi and photosynthetic algal cells. These organisms are one of the most diverse components of the Amazon forest (Sipman and Aptroot 2001, Lucking *et al.* 2009). The corticolous and foliicolous groups are much more diverse than the saxicolous species (Lucking 2008). The excessive amount of litter in these forests limits the diversity of terrestrial lichens; however, there are some records of them on the banks or landslides on the sides of roads.

Finally, mosses represent the dominant vegetation cover in a wide range of ecosystems, especially those that thrive in cold stress environments, where they typically adopt a cushion shape. However, the diversity of mosses 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 (Gradstein *et al.* 2001). In general, knowledge about the diversity of cryptogams is very limited (Scott *et al.* 1987, Brehm *et al.* 2008). Therefore, a comparison of the Amazon with the tropical Andes and surrounding areas can only be based on estimates using the high turnover in species composition along elevation gradients. The diversity of this group of plants could be related to climatic, edaphic, and floristic factors, but it is constant humidity that favors the growth of this group of plants (Chaverri-Polini 1998).

3.2.3 Diversity of insects

Although insects dominate terrestrial ecosystems (by the number of species or total biomass), the richness of insects in the region is completely unknown (Adis 2007, Hanson and Nishida 2016). Amazonian entomofauna is amazingly rich all along vertical forest strata, and it would be expected that the patterns of distribution of species at large spatial scales are not even across the region (Lucky *et al.* 2002, Erwin *et al.* 2005). High numbers of species coupled with high population densities are attributed to Amazonian insects, especially those inhabiting the forest canopy (e.g., Adis *et al.* 1998, Erwin 1998). For example, Formicidae (the ants) and Diptera (flies, mosquitoes, and their kin) represented 52% and 10%, respectively, of the more than 300 arthropods per square meter obtained by fogging the canopy.

In addition, a total of 95 different ant species were found on a single tree, as many as the entire indigenous ant fauna of Germany (Adis 2007). Very limited information is available about the centers of evolution and dispersal of insects, and other arthropods, that occur in the Amazon. Available data (*e.g.*, Erwin 1998, Adis 2007) suggests that some groups originated in the neotropics and are widely distributed beyond the borders of the Amazon (*e.g.*, leafcutter ants, *Atta* spp.); while other groups originated along the Andes or the Guyana shield, with a subsequent dispersal into the Amazon Basin (*e.g.*, Meinertellidae); and still others originated in the Amazon, along the floodplains of major tributaries (*e.g.*, some Carabidae).

Currently, it is difficult to predict whether changes in community composition are related to differences in vegetation types, soil, climate, human disturbance, or a very subtle combination of all of these factors. Probably, a different suite of factors affects different taxa and accounts for the observed patterns (*e.g.*, Erwin *et al.* 2005, Oliveira *et al.* 2010, Solar *et al.* 2016). In contrast to the amount of information available for terrestrial insects and arthropods, aquatic arthropod communities are much better known as a result of monitoring of water quality (*e.g.*, Heckman 2011, Hamada *et al.* 2014).

Many studies of Amazonian aquatic insects have examined water quality because of the insects' sensitivity to forest loss and other anthropic changes (Hamada *et al.* 2014), particularly the larval forms of groups such as Ephemeroptera, Trichoptera, Diptera, Plecoptera, and Odonata (Brito *et al.* 2020). Deforestation-induced reduction of aquatic insects can also affect the ichthyofauna, because aquatic larvae of many insects are the principal source of food for many small and medium species of fishes. One of the biggest challenges is to systematize the taxonomic kno-wledge of aquatic insects and other macroinvertebrates (Hamada *et al.* 2014) in the different aquatic ecosystems of the Amazon.

The high diversity of aquatic fauna is associated with the environmental heterogeneity of aquatic Amazonian ecosystems. Species from ten insect orders are specialized aquatic or semi-aquatic habits. The order Diptera stands out, which holds half of the known aquatic insects, notably Chironomidae (Trivinho-Strixino 2019). Several taxa are considered aquatic bioindicators because of their dependence on the aquatic environment for at least some stage of their life. The maintenance of riparian forests prevents the loss of species and ecosystem services provided by aquatic insect communities (Dala'Corte *et al.* 2020, Dias-Silva *et al.* 2020). When updating the list of Trichoptera, Paprocki and França (2014) found an increase of more than 65% in the number of species, of which 90%

Box 3.1 Domestication of plants and human influence

The Amazon Basin has a long history of human occupation, and cultivation and domestication of numerous plants (Young *et al.* 2007, Pearsall 2008, Piperno 2011, Clement *et al.* 2016) (Figure B3.1.1). At the time of European contact, over one hundred native plant species were already cultivated both in the high Andes and lowland Amazon, including beans, cacao, manioc, chili peppers, peanuts, potato, sweet potato, numerous fruit trees, palms, and many other tropical American species introduced to the region (Pearsall 2008; Piperno 2011; Clement et al. 2010, 2015; Levis et al. 2017; Lombardo et al. 2020). However, the imposition of colonial European agricultural methods and crops from the eastern hemisphere relegated most of those native species to local consumption and only a handful became of worldwide importance (National Research Council 1989, Ulloa Ulloa 2006, Young et al. 2007). However, a few species still have high importance in the region (Alexiades and Shanley 2004, Shanley et al. 2011 FAO).

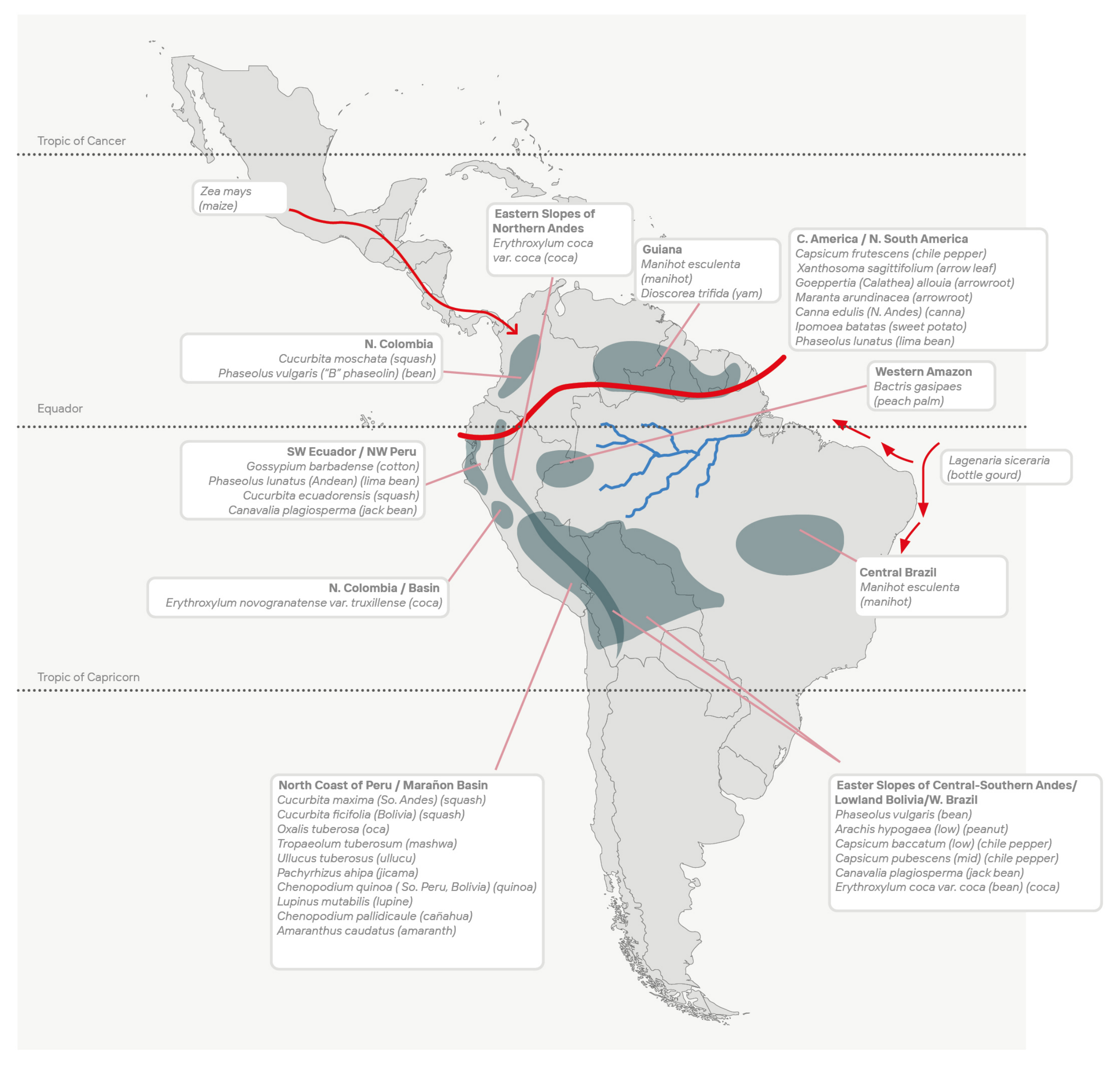


Figure B3.1.1 Areas of origin of domesticated plants (adapted from Pearsall, 2008).

The Andes region provided the world with the potato (*Solanum tuberosum* complex), tomato (*Solanum esculentum*), bell pepper and *ajíes* (*Capsicum* spp.), and beans (*Physallis* species), selected and genetically-manipulated beginning thousands of years ago (Raimondi and Camadro 2003, Rodríguez-Burrouzo *et al*. 2003, Pearsall 2008).

Lesser-known tuber species include *Arracacia xanthorrihiza* (aracacha, zanahoria blanca), *Oxalis tuberosa* (oca), *Tropaeolum tuberosum* (mashua), and *Ullucus tuberosus* (melloco or ulluco) (National Research Council 1989). Among the pseudocereals, *Chenopodium quinoa* (quinua) has recently arrived in international markets and has become an important food in gluten-free diets. Fruit trees originating from the Andes are the tree tomato (*Solanum betaceaum*), papaya (*Carica* papaya), lucuma (*Pouteria lucuma*), various species of the legume genus *Inga*, and shrubs such as naranjilla (*Solanum quitoense*), sweet cucumber (*Solanum muricatum*), goldenberry or uvillla (*Physalis peruviana*), and no fewer than ten species of passion fruits (maracuyá, species of *Passiflora*). Some of these plants have made their way into international markets through cultivation in New Zealand and California (Young *et al.* 2007).

Among multipurpose plant species that have been derived from human propagation and selection are the palms (Arecaceae). Palm species in the Amazon were first reported by Wallace (1853) as being useful to local inhabitants, and this was the first of a series of regional efforts on ethnobotanical research, at the local and regional levels, and assessments of domestication examples (Clement et al. 2010). When palm harvest takes place on communal properties, peasants overexploit their resources (Balslev et al. 2015). The majority of native palms from the tropical Andes (Colombia to Bolivia, 67% of the 336 species) have different uses and applications including food, construction, and oil (Valencia et al. 2013, Moraes et al. 2015). While exploring Venezuela, Humboldt and Bonpland (1805) collected and described to science the Brazil nut, *Berthollettia excelsa* (Lecythidaceae), a species of tree already well known long before the arrival of European explorers, and widely spread across the lowland Amazon. Recent analyses of tree species composition of lowland Amazonian forests revealed "hyperdominance" of a few species, particularly domesticated species such as the Brazil nut and various palm species, indicating that modern tree communities in the lowland Amazon may be structured, to an important extent, by a long history of plant domestication by Amazonian peoples (ter Steege et al. 2013, Levis et al. 2017). Forest patches dominated by one or a few useful plants are possibly the result of management practices over millenia (such as controlled burning, seed planting, or soil improvement) that have altered plant species composition (Levis et al. 2018, Silva et al. 2021). Other case studies show that the Amazon offers an impressive list of categories of useful plants that have also been part of domestication processes. *Bixa orellana*, achiote or annatto, long used in tropical America and worldwide in the cosmetic industry and as food coloring, was probably domesticated in northern South America (Moreira et al. 2015). Recent research revealed traces of cacao (*Theobroma cacao*) in an archeological site in the foothills of the Ecuadorian Andes dating back 5,300 years (Zarillo et al. 2018). The use of *Anadenanthera colubrina* (vilca, curupay, Fabaceae) powder — a psychoactive South American plant with a wide distribution — may have been particularly important for the Tiwanacota culture (600–1,000 A.D.) in Bolivia near Lake Titicaca (Pochettino et al. 1999); its use was then widely disseminated, coinciding with seasonal dry forests between 300—2,200 m (Kvist and Moraes 2006). The Amazon basin is a center of diversity for cotton, such as the most widely distributed *Gossypium barbadense* (Malvaceae), which is the second most cultivated species, and known for the best fiber quality (Liu *et al.*2015). Important crops likely originating in the southwestern Amazon are manioc (*Manihot esculenta*), peach palm (*Bactris gasipaes*), and peanuts (*Arachis hypogea*) (Clement et al., 2016). The most important medicine from the Andes is quinine (cascarilla, quinina), irrationally exploited and used for centuries to control malaria (Crawford 2016; Ortiz Crespo 1995, 2002; Ulloa Ulloa 2006 [2007]). Originally extracted from the bark of the cloud forest tree genus *Cinchona*, the alkaloid is nowadays synthetically produced and found in the bitter flavor of tonic water (Ulloa Ulloa 2016 [2007). The coca plant (*Erythroxylum coca*) grows on warm Andean slopes, and the leaves have been socially chewed or drunk as tea (mate de coca) for centuries, especially in Peru and Bolivia, as a stimulant, and to help with the effects of high-altitude sickness.

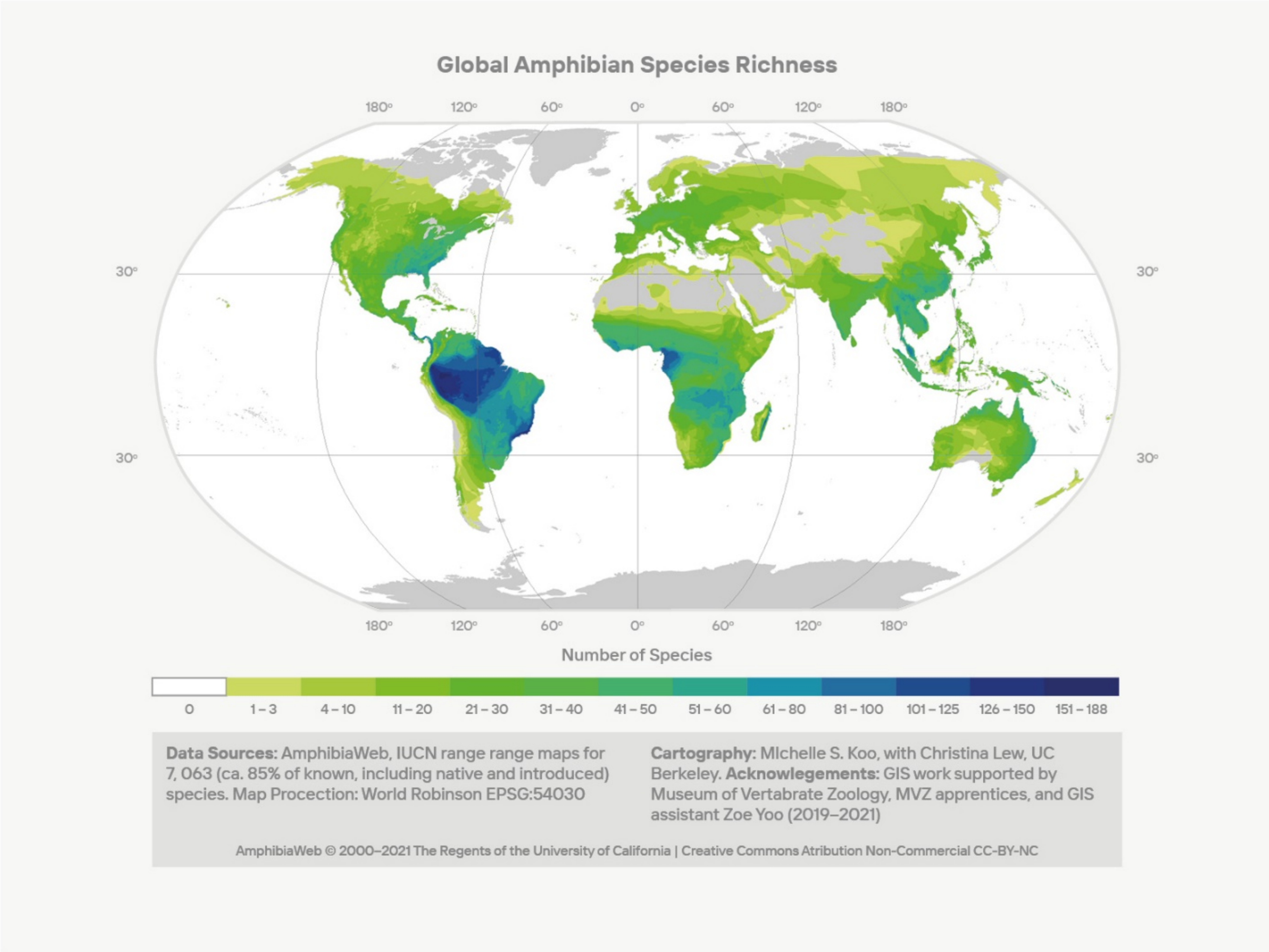
were new species to science, in addition to new records for Brazil. Elmidae, one of the four largest aquatic Coleoptera families, had the first checklist of Amazonian Elmidae species published in the last decade by Passos *et al.* (2010). There is an increasing number of new records and descriptions of genera and species for the Amazon region (*e.g.*, Menezes *et al.* 2018, Almeida *et al.* 2020). However, much is still unknown. The formation of taxonomists, strengthening of collections, and a continuous increase in the rate of description of new species can reduce this knowledge gap (Rafael *et al.* 2009).

3.2.4 Diversity of fish

The Amazon basin contains the world's most diverse freshwater-strict fish fauna, with 2,406 valid species belonging to 514 genera, 56 families, and 18 orders (Jézéquel *et al.* 2020). This exceptional diversity, which represents approximately 15% of the world's freshwater fishes, includes 58% of species found nowhere else on earth (1,402 endemics, Jézéquel *et al.* 2020). Part of this diversity also includes marine taxa that have adapted to freshwater, such as the diverse Amazon stingrays. Unlike many other river basins of the world, where species richness increases downstream along fluvial gradients (Muneepeerakul *et al.* 2008, Ibañez *et al.* 2009), species diversity and endemism show decreasing west–east gradients in the Amazon Basin, suggesting that contemporary Amazonian fish fauna originated in and colonized from the western portion of the Basin (Oberdorff *et al.* 2019). This pattern of fish diversity also indicates that the colonization of the eastern portion of the Basin is still incomplete and is interpreted by the authors as consistent with the recent establishment of the modern Amazon River in roughly the last 2.5 Ma, a topic still largely debated.

The importance of species richness to ecosystem stability, function, and resilience depends on the diversity and values of the species' traits (functional diversity), and on the degree of functional redundancy (degree of similarity in the functional characteristics) among species assemblages (Flynn *et al.* 2009, Mouillot *et al.* 2013, Kelley *et al.* 2018). The Amazon Basin not only has the world highest freshwater fish diversity, but also the highest functional diversity (Toussaint *et al.* 2016). Although functional diversity usually increases with taxonomic diversity, the functional diversity of Amazonian fish fauna is much larger than expected from its already exceptional diversity (Toussaint *et al.* 2016), probably reflecting the extremely rich variability of local environmental conditions (Leitaõ *et al.* 2018, Benone *et al.* 2020).

Fish species diversity in the Amazon Basin includes a large array of forms (including dorso-ventrally or laterally flattened, anguilliform, or globe-shaped species), colors, adaptations (*e.g.*, to the low oxygen concentrations found in floodplains), trophic habits (blood sucking, scale eating, or the arahuana [*Osteoglossum bicirrhosum*] jumping several meters out of the water to feed on insects, spiders, birds, or reptiles on tree branches), and reproductive adaptations (*e.g., Copeina arnoldi* that spawn on terrestrial plant leaves, reviewed in Carvalho *et al.* 2007). It also includes a wide variety of sizes, from miniature species that either mature under 20 mm of standard body length or do not exceed a maximum of 26 mm (Weitzman and Vari 1988), to large species that reach 3 m or more in length, like the pirarucu (paiche, *Arapaima gigas*) or the goliath catfish *Brachyplatystoma filamentosum*, both weighing more than 200 kg (Nelson 1994, Lundberg and Littmann 2003). Many of the small and miniature species are exploited as aquarium fish and sustain an important international ornamental trade, where the main export markets are Asia, Europe, and North America (Andrews 1990, Anjos *et al.* 2009, Evers *et al.* 2019). This trade also includes some large species that are caught and exported in juvenile stages, such as many pimelodid catfishes (*Brachyplatystoma* spp., *Pseudoplatystoma* spp., etc.), or the Amazonian arowanas (Moreau and Coomes 2006). In contrast, medium-sized and large species (mostly belonging to the Order Characiform and Siluriform, but also Perciform, Cichliform, Clupeiform, or Osteoglossiform) support important fisheries throughout the Basin and serve as an economic sopportunity and main source of animal protein for many of the inhabitants of the Amazon Basin (Barthem and Goulding 2007, Duponchelle *et al.* 2021).


Global Amphibian Species Richness

Data Sources: AmphibiaWeb, IUCN range range maps for 7, 063 (ca. 85% of known, including native and introduced) species. Map Procection: World Robinson EPSG:54030

Cartography: MIchelle S. Koo, with Christina Lew, UC Berkeley. **Acknowlegements:** GIS work supported by Museum of Vertabrate Zoology, MVZ apprentices, and GIS assistant Zoe Yoo (2019–2021)

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Figure 3.3 Global species richness of amphibians. Note the high alpha diversity in the lowland Amazonian rainforest. Source: AmphibiaWeb (2020).

3.2.5 Diversity of Amphibians

Amphibians are an ecologically and behaviorally diverse group of vertebrates containing 8,380 species (Frost 2021) that range from the familiar (frogs, toads, and salamanders), to the fossorial caecilians (Duellman and Trueb 1986, Wells 2013) (Figure 3.3). The Amazon Basin exhibits the highest density of species in the world, and one of the highest number of endangered species (AmphibiaWeb 2020, Bass *et al.* 2010, Scheele *et al.* 2019) (Figures 3.4 and Figure 3.5).

The diversity of Amazonian amphibians remains under-described. In addition to a sampling gap, which is largely associated with the remoteness of some of its habitats (Azevedo-Ramos and Gallati 2002), taxonomic reviews and inventories are insufficient to account for the diversity and distribution of Amazonian amphibians. Among Amazonian salamanders, for instance, the percentage of undescribed species is estimated to be as high as 400%, relative to the current number of known species (Jaramillo *et al.* 2020). In the Brazilian Amazon, amphibian diversity estimates increased 40% within three years (Azevedo-Ramos and Gallati 2002, Avila-Pires *et al.* 2007). This has implications for both basic and applied science, including the list of threatened species (Peloso 2010). For instance, comprehensive analyses of widely-distrib-

Figure 3.4 Amphibian diversity in the Amazon basin. (A) Embryos of the Andean glassfrog *Nymphargus wileyi*. (B) Torrent frog, *Hyloscirtus staufferorum*. (C) Tiger-striped Monkey Frog, *Callimedusa tomopterna*. (D) Amazonian salamander, *Bolitoglossa* sp. Photos by Tropical Herping.

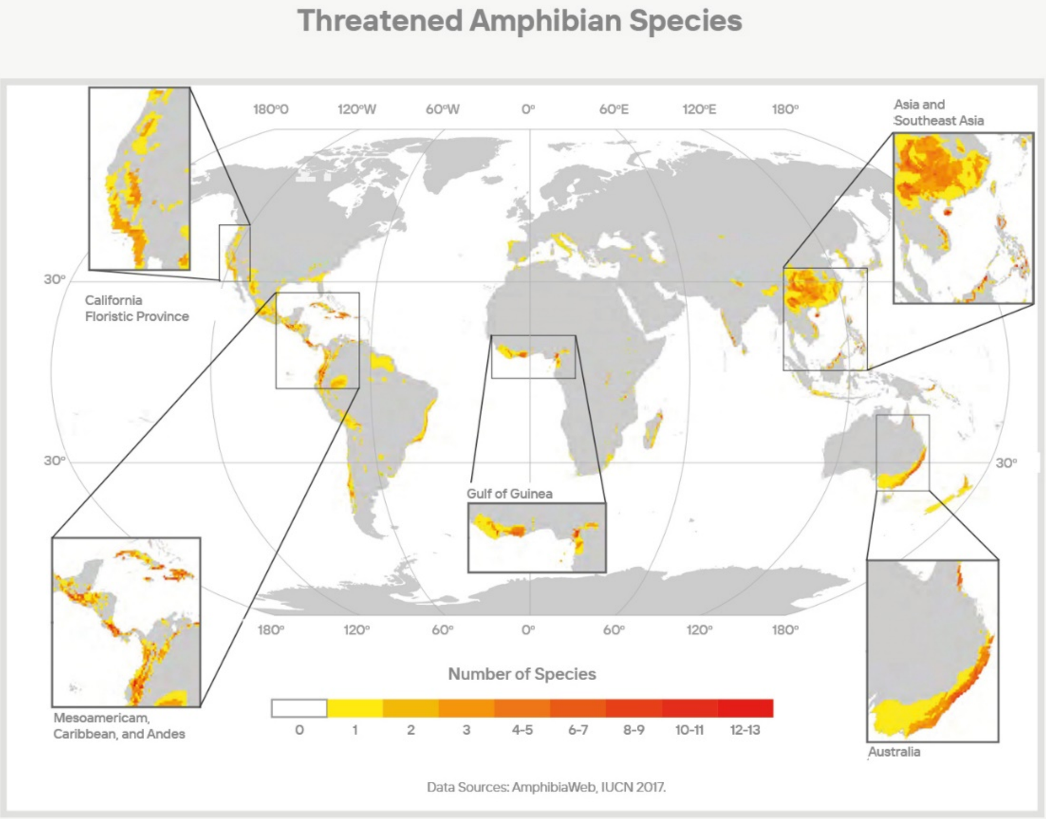

Figure 3.5. Threatened species of amphibians globally. Note that numerous species from the highlands of the Amazon Basin are endangered. Source: AmphibiaWeb (2020).

uted Amazonian amphibians frequently reveal rampant cryptic diversity, uncovering many species of smaller ranges within what was once assumed to be a single, widely distributed species (Funk *et al.* 2012, Fouquet *et al.* 2007, Jaramillo *et al.* 2020, Vacher *et al.* 2020). Amphibian biodiversity patterns display considerable variation within the Amazon Basin, often driven by the combined impact of topography, hydrology, evolutionary history, and the ecology of local species (Fouquet *et al.* 2015). 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 (Frost 2021, Guayasamin *et al.* 2020). Rivers appear to function as barriers to some amphibian taxa (especially non-riparian species, Moraes *et al.* 2016), but not all (Gascon *et al.* 2000). Their impact on the distribution of lineages can be river-specific (Funk *et al.* 2007b, Ortiz *et al.* 2018, Ferreira *et al.* 2020) and depends on the ecology of the species (Fouquet *et al.* 2015). The uplift of the Andes and the resulting lowland geological dynamics may have influenced patterns of amphibian diversity in the Amazon, as supported by a study of shifts in species composition along river transects (Gaston *et al.* 2000). DNA-based studies support the idea that lowland Amazonian communities were part of a connected set of Neotropical ecosystems, which they repeatedly colonized more than 10 million years ago. Colonizing amphibians, especially from the Andes, contributed new lineages to adjacent areas (Santos *et al.* 2009).

To preserve the diversity of amphibians of the Amazon Basin is to maintain their key ecological roles, cultural value, unique evolutionary histories, and also a potential for bioprospection (*e.g.*, in species with potent skin alkaloids such as the poison dart frogs; Badio and Daly 1994, Daly 1995, Rodríguez *et al.* 2017). However, given their extreme vulnerability to habitat destruction, climate change, and infectious diseases, amphibians are often considered at higher risk of extinction relative to other groups of organisms (Schee-le *et al.* 2019, Stuart *et al.* 2004, Wake and Vredenburg 2008).

3.2.6 Diversity of reptiles

Reptiles are among the most diversified vertebrate groups on the entire planet. Currently, 11,341 species have been recorded, in 92 families and 1,206 genera (Uetz and Hosec 2020). However, even with several studies carried out in the Amazon in the last decades, the diversity of species continues to be underestimated given the frequent discovery of new cryptic species, demonstrating that we are still unaware of the real diversity of this group (*e.g.,* Oliveira *et al.* 2016). The Amazon rainforest registers 371 species, occupying an immense number of terrestrial and aquatic environments (Mittermeier *et al.* 2003, Avila-Pires and Ramalho 2019). Reptiles have intriguing patterns of diversity and distribution throughout the entire Amazon Basin, such as the well-known patterns of distribution and diversity along latitudinal gradients and the west to east gradient (Da Silva and Sites 1995, Guedes *et al.* 2018, Roll *et al.* 2017).

In addition, squamata reptiles show an intriguing pattern of variation in species richness along a north–south gradient that runs from eastern Ecuador to southeastern Peru. For example, some studies carried out in the northwestern Amazon indicate a greater diversity of species in relation to locations in the southeast Amazonian plain (*e.g.,* Da Silva and Sites 1995). Recently, estimates of species richness obtained from different sampling locations, as well as from specimens obtained from scientific collections, suggest a greater richness of snake species in the northwestern Amazon compared with the southern region (Rabosky *et al.* 2016). In addition, these and other results imply that the alpha diversity for Squamata distributed to the north of the Amazon can be up to 30% greater in relation to the communities in the south (Da Silva and Sites 1995, Duellman 2005).

3.2.7 Diversity of birds

The Amazon hosts the highest number of birds in the world. With at least 1,300 species, of which approximately 265 are endemic, the Amazon harbors approximately 38% of the Neotropic's approximately 4,000 birds (Nores 2000, Mittermeier *et al.* 2003). The true number of bird species in the Amazon could be much higher. Relatively recent molecular systematic studies have revealed that traditionally accepted species often group several genetically divergent lineages representing new cryptic species together (Milá *et al.* 2012). Bird diversity increases in proximity to the Andes. The 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 birds reach their lowest elevational range (Nores 2000, 2011). For several decades, scientists have been trying to understand the geographic structure of bird communities and the underlying causes for observed patterns of speciation (*e.g.*, Haffer 1969, Bates 2001, Pomara *et al.* 2014, Ribas and Aleixo 2019).

The evolution of Amazonian birds is a complex process, but molecular systematics and phylogeographic studies suggest that many avian lineages diversified recently during the late Tertiary and early Quaternary (Weir 2006, Aleixo and Rossetti 2007, Silva *et al.* 2019). This period coincides with large landscape changes (*e.g.*, Colinvaux 1993, Haffer 1993, Bush 1994, Marroig and Cerqueira 1997). It appears, during the Pliocene, ancestral bird faunas occupied mostly upland forested habitats in the northern and western Amazon. After a series of interactions between climate-driven dynamics and riverine barriers, avian lineages started separating on opposite sides of the region, Negro and Madeira rivers (the most ancient rivers in the Basin). These changes in climate and connectivity affected bird populations differently, depending on their ecological requirements and degree of habitat specialization. As a result of this processes, currently, the wetter western Amazon contains older and richer bird faunas compared with the dryer eastern Amazon (Silva *et al.* 2019). However, knowledge of the evolution of Amazonian birds is a complex process and data are still fragmented. More sampling is needed to understand regional patterns of bird species richness and community composition in the Amazon (Oliveira *et al.* 2017).

3.2.8 Diversity of mammals

The Amazonian region harbors one of the richest mammalian faunas of the world, with approximately 140 genera and 425 species (Mittermeier *et al.* 2003). Amazonian mammals account for approximately one-third of all South American mammalian diversity, approximately 1,260 species (Bonvicino and Weksler, 2012). In addition, several locations in the Amazon have the highest alpha-diversity of non-volant mammals anywhere on Earth (Peres, 1999, da Silva *et al.* 2015). However, the number of species at any single locality in the Amazon significantly varies depending on forest types and habitat diversity. Mammal communities in seasonally flooded (*várzea*) forests, for example, 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* (Peres 1997, Haugaasen and Peres 2005). Endemism is also very high, with 10 endemic genera and 144 species of mammals (34% of total) found only in the Amazon (Pires *et al.* 2000, Solari *et al.* 2012). This impressive mammalian diversity is not distributed equally among orders. The high level of endemism of Amazonian mammal species is due mainly to the input of three orders, marsupials, rodents, and primates, which together comprise approximately 80% of all endemic species (Voss and Emmons 1996, Paglia *et al.* 2012).

Despite these figures, the mammalian fauna of this vast region is still under-sampled, and there are not enough exhaustive surveys of mammals. As a result, the spatial turnover of species assemblages at different scales remains poorly understood (Voss and Emmons 1996, Peres 1999, Solari *et al.* 2012). Based on mammal inventories carried out throughout the Amazon, it has been suggested that mammalian communities in the western Amazon are the most diverse in the region, the Neotropics, and probably the world. Explanations for this pattern include present-day ecological factors such as climate, habitat, and topographical heterogeneity; primary productivity; and ecosystem dynamics (Voss and Emmons 1996, Peres 1999; Machado *et al.* 2019). Mammals are considered well-known because the rate at which new species are discovered is low compared with other groups. However, in recent years several new species have been described and new records have extended the geographical ranges of some species by hundreds of kilometers (Patterson 2001, 2020). We are still learning about the fascinating diversity of Amazonian mammals, and this knowledge is critical for the conservation of the Amazon region.

The Amazon has experienced a dynamic process of transformation throughout its history, including marine transgressions and abrupt changes in the flow of its water bodies. The creation of geographical barriers, such as rapids and streams, has allowed many species to prosper and others to disappear. Among them, aquatic mammals play an important role. The dolphins of the genus *Inia* moved from the Atlantic to the center of the continent in Bolivia, where they were isolated about 3.1 million years ago by the Madeira River (Hollatz *et al.* 2011), while others dispersed throughout the Amazon and the Orinoco region. Currently, only the presence of the species *Inia geoffrensis* is recognized with two subspecies: *Inia geoffrensis geoffrensis* distributed in the Amazon and Orinoquia, and *Inia geoffrensis boliviensis* in Bolivia and the Madeira River (Da Silva *et al.* 2018). However, there is evidence to suggest that the Bolivian unit may be a different species (*Inia boliviensis*), and in the Tocantins/Araguia complex in Brazil *Inia araguiaensis* (Hrbek *et al.* 2014). Similarly, approximately 2.5 million years ago, the ocean level rose approximately 150 meters and generated another transgression of the sea into the Amazon, promoting the entry of another dolphin of the genus *Sotalia*. This species adapted to freshwater conditions, evolving to *Sotalia fluviatilis* approximately 1.2 million years ago. Also, there is evidence to suggest that during the Pliocene, some 4.5 million years ago, there was a displacement of manatees from the Atlantic to the Amazon, giving rise to the only species of freshwater manatee, *Trichechus inunguis*, distributed in Brazil, Colombia, Peru, and Ecuador (Domning 1982). Another important group of aquatic mammals in the Amazon are the otters; the giant river otter (*Pteronura brasiliensis*) and the Neotropical otter (*Lontra longicaudis*), whose origin seems to be associated with the geological, hydrological, and climatic changes that the region experienced during the Pliocene-Pleistocene.

3.2.9 Diversity of parasites and pathogens (and their interactions with mammalian hosts)

If the biodiversity of animals, fungi, and plants in the Amazon is still poorly known, much less can be said about the biodiversity of pathogens and parasites. Despite accounting for one-third to over half of the species on Earth (Poulin 2014), these organisms are usually ignored in biodiversity inventories and conservation studies (Gómez and Nichols 2013). Most of the current knowledge is highly biased to parasites that cause human, domestic animal, or plant diseases (Gómez and Nichols 2013). Nevertheless, parasites and pathogens play an important role at individual, population, and ecosystem levels (Wood and Johnson 2015), such as modulating the immunity of hosts and the dynamics of their populations, altering the composition of ecological communities, and modifying trophic interactions, including predation rates and nutrient cycling. These processes have complex effects, both direct and indirect, which may include cascade effects and co-extinctions, whose implications are not yet completely understood (Strona 2015).

Despite the significance of parasite biodiversity, the actual richness of most parasitic groups remains largely unknown. When accounting for the biodiversity of mammal parasites in the Amazon region, we found that from the 425 wild mammals, only 185 species have been studied regarding their interactions with parasites. Brazil is the country that published the largest number of studies on mammal-parasite interactions, followed by Peru, French Guiana, Bolivia, Venezuela, Guyana, Ecuador, and Colombia. The mammal species with the highest richness of studied parasites are the marsupial *Didelphis marsupialis*, the bat *Carollia perspicillata*, and the primates *Sapajus apella* and *Saimiri sciureus*. However, most of those studies report interactions with a single parasite species; studies investigating the community composition of parasites or co-infections are rare (Conga *et al.* 2014). Protozoans are the parasite group with the largest number of studies (84 publications), but are not the group with the highest richness of species. The parasite group with the highest number of species reported interacting with wild mammals are helminths (77 species), arthropod ectoparasites (65 species), viruses (62 types), protozoans (29 species), bacteria (12 species), and fungi (seven species).

Table 3.2 Most studied parasite and pathogen species in the Amazon.

Parasite Groups	Most Studied Species	References
Virus	*Rabies lyssavirus,* Laguna negra orthohantavirus, Simian foamy virus	Deem and Emmons 2005, da Rosa *et al*. 2012, Carnieli Jr *et al.* 2013, Costa *et al.* 2013, Favoretto *et al*. 2013, Kobayashi *et al.* 2013, Muniz *et al*. 2013, de Barros Lopes *et al.* 2014, Oliveira *et al*. 2015, Pereira *et al.* 2017
Arbovirus	*Changuinola, Marituba, Mayaro, Oriboca, Oropouche*	Leduc *et al*. 1981, Figueiredo *et al.* 1988, de Thoisy *et al.* 2003, Silva *et al*. 2013, Silva *et al.* 2014, Hang *et al.* 2014, Nunes *et al.* 2018, Nunes *et al.* 2019
Bacteria	*Leptospira interrogans, Mycobacterium leprae*	Deem and Emmons 2005, da Silva *et al*. 2018, Stefani *et al.* 2019, dos Santos Medeiros *et al.* 2020
Helminth	*Dipetalonema gracile, Toxocara canis, Trypanoxyuris minutus, Trypanoxyuris trypanuris*	Hugot 1985, Bain *et al.* 1986, Tantalean *et al.* 1990, Hugot *et al.* 1996, Stuart *et al.* 1998, Hugot 1999, Noronha *et al*. 2002, Deem and Emmons 2005, Vieira *et al*. 2008
Protozoa	*Trypanosoma cruzi, Trypanosoma rangeli, Trypanosoma cruzi marinkellei, Trypanosoma dionisii, Toxoplasma gondii*	Deane 1961, Deane and Damasceno 1961, Ayala 1964, Baker 1972, Miles *et al.* 1981, Miles *et al.* 1983, Lanham *et al.* 1984, Póvoa *et al*. 1984, Carrasco *et al*. 1996, Ziccardi and Lourenço-de-Oliveira 1997, Stuart *et al*. 1998, de Thoisy *et al.* 2003, Deem and Emmons 2005, Dubey *et al.* 2007, Demar *et al.* 2008, Lisboa *et al.* 2008, Roque *et al*. 2008, da Silva *et al*. 2009, Marcili *et al.* 2009a, Marcili *et al.* 2009b, Marcili *et al.* 2009c, Ortiz *et al.* 2009, Cavazzana *et al*. 2010, Lewis *et al*. 2011, De Araujo *et al.* 2013, Monteiro *et al*. 2012, Roque *et al*. 2013, Acosta *et al*. 2014, Vitaliano *et al*. 2014, da Costa *et al.* 2015, Jansen *et al.* 2015, Lima *et al.* 2015, da Costa *et al.* 2016, dos Santos *et al*. 2017, Rodrigues *et al*. 2017, Jansen *et al.* 2018, Barros *et al.* 2019, Filgueiras *et al.* 2019, Pérez *et al*. 2019, Rodrigues *et al.* 2019, McClean *et al.* 2020
Ectoparasite	*Amblyomma ovale, Amblyomma naponense, Amblyomma geayi, Amblyomma cajennense, Amblyomma nodosum*	Stuart *et al.* 1998, Labruna *et al.* 2002a, Labruna *et al.* 2002b, Robbins and Deem 2002, Zerpa *et al.* 2003, Deem and Emmons 2005, Labruna *et al.* 2005, Robbings *et al.* 2009, Martins *et al*. 2013, Martins *et al.* 2014, Soares *et al*. 2015, Witter *et al.* 2016, Furtado *et al.* 2017, Zimmermann *et al.* 2018, Gruhn *et al*. 2019, Peckle *et al*. 2019
Fungi	*Histoplasma capsulatum, Pneumocystis carinii*	Lainson and Shaw 1975, Arias *et al*. 1982, Naiff *et al.* 1985, Naiff *et al.* 1996, Hugot *et al*. 2003

From those, 38 viruses, 16 arboviruses, 11 bacteria, nine helminths, 19 protozoans, one ectoparasite, and seven fungi are known to be zoonotic and cause disease in humans. The most studied parasites infecting wild mammals in the Amazon region are the protozoans *Trypanosoma cruzi* (the causative agent of Chagas disease in humans), *Plasmodium brasilianum*, *Trypanosoma cruzi marinkellei*, *Trypanosoma rangeli*, the virus *Rabies lyssavirus* (the causative agent of rabies in humans), and the ectoparasite *Amblyomma cajennense* (Table 3.2).

Concerning arthropod-borne viruses (or arboviruses), 27 different species have been recorded as infecting wild mammals in the Amazon. From those, 16 are known to be zoonotic, including the viruses Caraparu, Changuinola, Dengue, Guama, Mayaro, Marituba, Murutucu, Oriboca, Oropouche, Piry, Saint Louis, Tacaiuma, and Yellow fever. It is important to emphasize that in the Amazon region some of these zoonotic agents are also shared with domesticated mammal species such as pets and cattle, and that other zoonotic pathogens have already been identified in domesticated animals (e.g., Eastern Equine Encephalitis Virus and West Nile Virus). These domesticated species can play an important role in the transmission cycle of zoonotic agents (Johnson *et al.* 2020), especially when in high densities (e.g., livestock production), functioning as amplifying hosts and intermediating transmission to humans and wild animals. Given recent concerns about the risk of an emerging pandemic originating in the Amazonian region (Vale *et al.* 2021), current increasing rates of deforestation, the loss and homogenization of biodiversity, and increasing social vulnerabilities are major concerns. This, added to the gap of knowledge about the biodiversity of host-parasite interactions, elucidates the need for understanding and building resilience to emerging diseases as a top societal challenge and research priority.

3.3 Outstanding Ecological Processes and Adaptations in Terrestrial and Aquatic Ecosystems

3.3.1 Plant-animal interactions

Plant-animal interactions are a central ecological process in Amazonian forests, without which these forests would cease to exist: 80–90% of trees obligately rely on animals for seed dispersal (Gentry 1982, Hawes *et al.* 2020), and as many as 98% of plants obligately rely on animals for pollination (Bawa 1990). Animal dispersers are attracted to seeds by a wide variety of plant strategies, and birds, bats, mammals, fish, and insects are all important dispersers responding to and selecting for different plant strategies for attraction (*e.g.*, Howe and Smallwood 1982). Consumptive effects generate diversity through coevolutionary arms-races and control plant and animal biodiversity on ecological and evolutionary time scales. These networks of mutualists and consumers regulate all aspects of Amazonian forests, and are responsible for their composition, species regulation, recovery from disturbance, and the generation of biodiversity. Changes to species interactions can have cascading effects on Amazonian ecosystem function and the services they provide humanity, as briefly discussed below.

Seed dispersers and pollinators interact with plants, form mutualistic networks, and form the very architecture of Amazonian biodiversity (Bascompte and Jordano 2007). Seed dispersal moves seeds away from parent trees, cleaning them of pulp and in many cases physiologically altering them, all of which improve survival and increase genetic diversity (Howe and Smallwood 1982, Hardesty *et al.* 2006). Seed disperser communities are exceptionally complex (Jordano *et al.* 2007), and plant-disperser networks are comprised of many different modules of differing kinds of dispersers (Donatti *et al.* 2011), underscoring their importance of maintaining biodiversity in these systems (Kakishima *et al.* 2015). Vast areas of the Amazon are seasonally flooded, and fish have been shown to be critical dispersers in these forests and link terrestrial and aquatic processes (Goulding 1983, Correa *et al.* 2015a). Pollination networks in Amazonian forests are highly diverse and complex, include a wide variety of invertebrates and vertebrates, and form the basis of reproduction in the perpetuation of Amazonian forests (Bawa 1990, Bascompte and Jordano 2007). Pollinator networks are often highly specialized and are built with modules of interacting species with low redundancy, underscoring the role of pollinator biodiversity and conservation on overall Amazonian biodiversity and ecosystem services (Kremen *et al.* 2007, Olesen *et al.* 2007).

Trophic interactions are equally important, locking animals into networks of herbivory on leaves, seeds, and roots, with high degrees of specialization. Plant-herbivore coevolutionary interactions have led to the evolution of high species diversity by locking groups of organisms in evolutionary arms races of attack and defense (Ehrlich and Raven 1964), and have led to a spectacular diversification in Amazonian plant functional traits and chemical defenses that not only regulate and generate forest diversity, but also provide critical services for humanity (Coley and Barone 1996, Fabricant and Farnsworth 2001, FAO *et al.* 2011). Herbivore effects on plants depend on both geology and climate, and trade-offs in these interactions have generated landscape-level diversification of tropical trees (Fine *et al.* 2004, Fine *et al.* 2013). Plant-herbivore interactions have emerged as the key component in maintaining diversity in tropical forests, with frequency- and density-dependent effects at multiple scales (Janzen 1970, Harms *et al.* 2000, Terborgh 2012). All of these plant-animal interactions are embedded in food-webs of consumptive interactions, which in turn regulate them in Amazonian ecosystems, with direct regulation by predation, and indirect mutualisms arising from trophic cascades (Schmitz 2008, Terborgh and Feely 2009).

Plant-animal interactions are at high risk from multiple forms of human-caused change (*e.g.*, Sales *et al.* 2020, 2021). Disruptions to plant-animal interactions can have rapid effects on forest community composition, which has long-term consequences (Terborgh *et al.* 2001), changing forest composition as well as ecosystem function and services (Morris 2010). Defaunation has cascading effects on Amazonian forests through the direct effects of hunting and indirect effects of anthropogenic disturbances, particularly affecting large-bodied vertebrates (Bodmer *et al.* 1997). Defaunation affects all plant-animal interactions, especially disperser and seed predation networks, with significant consequences for Amazonian tree diversity (Kurten 2013, Peres *et al.* 2016); ecosystem function and services, particularly carbon storage (Markl *et al.* 2012, Bello *et al.* 2015); nutrient cycling (Stevenson and Guzmán-Caro 2010, Doughty *et al.* 2016); and even biogeography (Doughty *et al.* 2016). Deforestation and forest fragmentation can have effects beyond simple removal of trees, with effects cascading through pollination (Wirth *et al.* 2008, Barlow *et al.* 2016, Lister and García 2018), dispersal (Laurance *et al.* 2006, Markl *et al.* 2012, Caughlin *et al.* 2014, Hawes *et al.* 2020), and consumptive networks (Terborgh 2013), fundamentally changing the ecological interactions that maintain and generate Amazonian biodiversity. Plant-animal interactions are particularly vulnerable to climate change effects, both directly through disruption of plant-animal interaction networks due to differential responses to climate among components (Primack *et al.* 2009, Salcido *et al.* 2020), and indirectly by exacerbating the effects of defaunation and forest degradation (Valladares *et al.* 2006, Barlow *et al.* 2016). An overwhelming and central result from the study of Amazonian forests is that intact plant-animal interaction networks are essential for the resilience of forest biodiversity to anthropogenic changes, and for the recovery and restoration of Amazonian systems.

3.3.2 Flood pulses and nutrient flow

Aquatic ecosystems in the Amazon are a complex mosaic of habitats influenced by flood pulses and by the pattern of nutrient flow. This has generated areas with high and low productivity, which have promoted complex adaptation processes in aquatic organisms. Fish are undoubtedly one of the most relevant cases, supporting large biomass in highly productive rivers (white-water), such as the Amazon, Madeira, Caquetá/Japurá, Putumayo, and Purus, and low biomass but high species richness in rivers of black- and clear-waters. In the latter, the fish depend more on external sources of food (fruits, seeds, insects) or on trophic subsidies provided by migratory fishes (see Section 3.3.3). Given the transparent conditions in clear- or black-waters, fish usually develop intense colors with an important function for reproduction (Borghezan *et al.* 2021).

Many species that live in floodplains have special adaptations to withstand low oxygen levels and high temperatures during periods of drought (Junk *et al.* 1983, Val 1995, Val and Almeida-Val 1995, Val *et al.* 2015). However, other species choose to perform lateral migrations towards main channels for reproductive purposes, spawning in the main channels and then returning to lakes and small tributaries. These fish are predominantly from the Prochilodontidae and Curimatidae families. Species such as the pirarucu (paiche, *Arapaima gigas*), which are apparently sedentary, 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 flooded forest, where the males exercise parental care of their young (Castello 2007).

Large aquatic carnivores, such as the Amazon river dolphin (*Inia geoffrensis*), sometimes follow fish migrations, ensuring permanent and abundant access to prey. In general, the females seem to be more resident and are associated with systems of lakes and confluences where they take care of their young, while males make long migrations in search of food and reproductive options (Trujillo *et al.* 2018). In adaptive terms, the Amazon river dolphin has developed a better ability to search for fish in the flooded forest than its sympatric species, the gray dolphin (*Sotalia fluviatilis*). The cervical vertebrae of their neck are not fused, allowing them to move their heads, which, combined with a long snout, allows them to catch benthic or pelagic fish that hide under macrophytes or among submerged vegetation. Likewise, a low dorsal fin and pectoral fins with great movement capacity allow them to move very well in the flooded forest. Something similar occurs with giant otters (*Pteronura brasiliensis*), which make up family groups of between 6 and 14 individuals. They are mainly located in tributaries and lagoons and have more or less well-defined territories during the low water period, but when the water level increases, the fish disperse in the flooded forest and the size of the territory increases.

During periods of low water, large stretches of beaches are exposed and are the ideal habitat for the massive spawning of several species of turtles, especially of the genus *Podocnemis*, such as the Giant Amazon River Turtle (*Podocnemis expansa*) and Yellow-Spotted River Turtle (*Podocnemis unifilis*). The reproductive success of these species depends, to a great extent, on the characteristics of the beach, mainly the type of sediment and the height at which the nests are dug, as there are frequent rises in water levels that can affect nests in lower parts. Another species that has adapted to flood pulses in the Amazon are jaguars (*Panthera onca*), which were thought to move to non-flooded areas during these periods. Recent studies show that in areas such as Mamirauá in Brazil, they can spend up to three months living in the treetops, feeding primarily on sloths, alligators, and even giant otters (Ramalho 2012, Alvarenga *et al.* 2018).

3.3.3 Fish migrations

Migratory fishes play important ecological roles in Amazonian aquatic food webs, providing crucial subsidies from one component of the ecosystem to the other, either as predators or prey, or as engineers or seed dispersal agents. Therefore, modification or disruption of their migratory patterns by overharvesting, impoundment, or habitat degradation is likely to profoundly alter ecosystem processes by modifying trophic cascades, primary production, detrital processing, and subsidies transfer over wide spatial scales (Flecker *et al.* 2010, Barthem *et al.* 2017, Anderson *et al.* 2018).

Amazonian goliath catfish of the genus *Brachyplatystoma* perform the world's longest known freshwater migration. 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 areas in the Andean piedmont of Bolivia, Colombia, Ecuador, and Peru, to its nursery in the estuary in Brazil (Barthem and Goulding 1997, Barthem *et al.* 2017, Duponchelle *et al.* 2016, Hauser *et al.* 2020). This exceptional migration involves natal homing, a behavior seldom observed in freshwater, but common in species migrating between the sea and rivers, such as salmon. In this process, adult fish usually return to the watershed where they were born either in the upper Madeira (Duponchelle *et al.* 2016) or in the upper Amazon (Hauser *et al.* 2020). Together with river dolphins, goliath catfish are the apex predators of Amazonian rivers (Barthem and Goulding 1997) and several species are overharvested (Barthem *et al.* 1991, Petrere *et al.* 2004, Agudelo *et al.* 2013). As demonstrated in both marine and freshwater ecosystems, top predators play essential ecological functions and the depletion of their populations can entail profound modifications of ecosystems through trophic cascades (Baum and Worm 2009, Chase *et al.* 2009, Frank *et al.* 2005, Persson *et al.* 2007). Similar cascading effects are expected with the decline of the large goliath catfish community in the Amazon Basin (Angelini *et al.* 2006, Lima 2017), which could be further accentuated by their exceptional migratory behavior (Borer *et al.* 2005).

Fish migrations, and in particular the movements of detritivorous fishes, also play crucial ecological roles in nutrient transport, with important consequences on local food web dynamics. Fishes of the family Prochilodontidae (*Prochilodus* and *Semaprochilodus*), which feed on detritus, algae, and associated microorganisms (Bowen 1983), indeed perform complex, large-scale migrations from nutrient-poor tributaries (black- or clear-waters) during the low water period to the rich floodplains of white-water tributaries for spawning and feeding during high waters (Ribeiro and Petrere 1990, Vazzoler and Amadio 1990, Vazzoler *et al.* 1989). Their movements between different river systems connect food webs over large spatial scales and result in important energy and biomass transfer into oligotrophic waters, where these species are preyed upon by large piscivores that could normally not support high population densities without these subsidies (Hoeinghaus *et al.* 2006, Winemiller and Jepsen 1998). Although this phenomenon has mainly been studied in Prochilodontid fishes, flows of primary production from nutrient-rich white-water rivers into clear- or black-water rivers by migratory detritivorous species is likely widespread in the Amazon Basin, as many other migratory characids, such as *Anodus* spp., *Brycon* spp., *Colossoma macropomum*, *Leporinus* spp., *Mylossoma* spp., *Triportheus* spp. spawn and grow exclusively in white-water, but can live in any water type as adults (Lima and Araujo-Lima 2004). Another striking case is the annual migration of the juvenile pencil catfish, *Trichomycterus barbouri* (~3 cm), which consists of hundreds of thousands of individuals moving from their nursery area in the downstream Béni River to its upper reaches hundreds of kilometers upstream (Miranda-Chumacero *et al.* 2015). This migration provides a source of food for fish, water birds, reptiles, and human populations along the way.

Many Amazonian 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 that falls into the water, dispersing seeds over large distances while improving their germination process (Goulding 1980, Correa and Winemiller 2014, Correa *et al.* 2015a). Most of the approximately 150 known frugivorous fish species in the Neotropics, belonging to 17 families and 6 orders, also occur in the Amazon Basin (Horn *et al.* 2011). They can consume at least 566 species of fruits and seeds from 82 plant families, thereby contributing to their spatial distribution and biodiversity (Correa *et al.* 2015a). Because commercial fisheries primarily target large-bodied species, which can disperse seeds of a broader size range and of a higher diversity of plants, overharvesting could threaten not only fruit-eating fish populations, but also the biodiversity and conservation of the flooded forest (Correa *et al.* 2015b).

3.3.4 Environmental variation and adaptation of organisms

Of the 7 million km^2 covered by the Amazon region, 800,000 km^2 are aquatic ecosystems. The interaction between land and water responds to a delicate climatic gear that is responsible for the flood pulse (Junk *et al.* 1989). This is undoubtedly one of the most important and relevant environmental processes in the Amazon, since it generates variations of up to 15 m in the vertical plane and thousands of kilometers of flooding in the lateral plane. This clearly marks a low-water period and a high-water period, with transition periods throughout the year. This cycle, repeated for thousands of years, has generated exceptional adaptation processes by fauna and flora. A good part of the vegetation is adapted to being submerged for several months and synchronizing its fruiting processes in high waters as a dispersal strategy. Likewise, during this period, the proliferation of macrophytes and large patches of aquatic vegetation serve as a refuge for fish and other organisms and provides food for species such as manatees and capybaras (Parolin *et al.* 2004, Piedade *et al.* 2010, Junk *et al.* 2011).

Changes in the water level also generate a mechanism that triggers the lateral migration of many species, including fish, dolphins, and manatees (Cox-Fernandes 1997, Martin and da Silva 2004, Arraut *et al.* 2010). In the case of dolphins, in high waters, they disperse into the flooded forest, tributaries, and lagoons in search of food, but when the water level begins to decrease, gray dolphins (*Sotalia fluviatilis*) move to the main rivers and later Amazonian dolphins (*Inia geoffrensis*) do as well to avoid being trapped in bodies of water with a low supply of food. Shallow waters represent the time of greatest availability of food in the main rivers. With the contraction of the entire system, the fish are contained in a smaller space and dolphins take advantage of this to feed. This increase in energy allows reproduction to be synchronized with the season. The young are born 13 months later, also in periods of low water levels. In contrast, manatees benefit from higher macrophyte production in high water periods, while in summer they must browse submerged logs for algae and subsist on body fat reserves.

3.4 Genetic Plasticity and Molecular Diversity

Because species delimitation is based on genetic variation, natural selection, and adaptation (Sexton *et al.* 2009), species richness is widely regarded as a fundamental measure of biodiversity at the general level (Gotelli and Colwell 2001). Patterns of genetic variation in species also represent a vital but often underestimated component of Amazonian biodiversity; phylogenetic diversity assesses the evolutionary and cumulative distinctiveness within and between areas and taxa (Antonelli *et al.* 2018a). Phylogenetic diversity measures the total amount of evolution per lineage over time among all members of a clade or area (Tucker *et al.* 2017). In general, this has been shown to provide a better estimate of feature divergence than species richness alone (Forest *et al.* 2007).

Although many groups of organisms are widely distributed in tropical regions, the detailed pattern of variation in species (Costa and Magnusson 2010), including spatial, genetic, and morphological variation, and their genetic structure have recently been documented, corresponding to several independent evolutionary units (Ribas *et al.* 2012, Schultz *et al.* 2017). Genetic diversity of terrestrial mammals and amphibians is 27% higher in tropical areas, and disturbed habitats have less genetic diversity compared to undisturbed areas (Miraldo *et al.* 2016). Well-sampled molecular phylogenies have recently been developed to reveal the evolution of tropical biota (Dexter *et al.* 2017, Eiserhardt *et al.* 2017). Molecular sampling at the intraspecific level (subspecies and populations) has significantly advanced in the Neotropics (Antonelli *et al.* 2018b). According to the analysis of dated molecular phylogenies, it has been shown that some Neotropical regions may be more permeable to immigrating lineages than others. Furthermore, the intrinsic differences between taxonomic groups (such as dispersal capacity) may allow some lineages to colonize new regions (Antonelli *et al.* 2018b), despite niche conservatism (Crisp *et al.* 2009), and others support adaptations to ecological changes (Simon *et al.* 2009, Trujillo-Arias *et al.* 2017). However, for most taxonomic groups of the Amazon, knowledge about biotic exchanges and dispersal histories remains surprisingly poor, and it is not understood which regions served as primary sources and sinks of biodiversity, defined as providers and recipients (Antonelli *et al.* 2018b). It has been concluded that the Amazon is the main Neotropical diversity source of angiosperms, ferns, snakes, birds, mammals, and frogs for other regions, providing >2,800 lineages (63% of all dispersal events), being approximately 4.6 times the second most important source of diversity (Antonelli *et al.* 2018b, Figure 3.6).

As it is known, both the western and central Amazon have the highest species richness of tree communities (ter Steege *et al.* 2003, Chave *et al.* 2007) and, therefore, the highest phylogenetic diversity, but the lowest mean nearest taxon distance (Honorio Coronado *et al.* 2015). The mean pairwise phylogenetic distance between species is correlated with how evenly taxa are distributed among the three principal angiosperm clades (Magnoliids or Dicots, Monocots, Eudicots) and are both the highest in the western Amazon. Finally, seasonally dry tropical forests and forests on white sands have low phylogenetic diversity (Fine *et al.* 2010, Honorio Coronado *et al.* 2015).

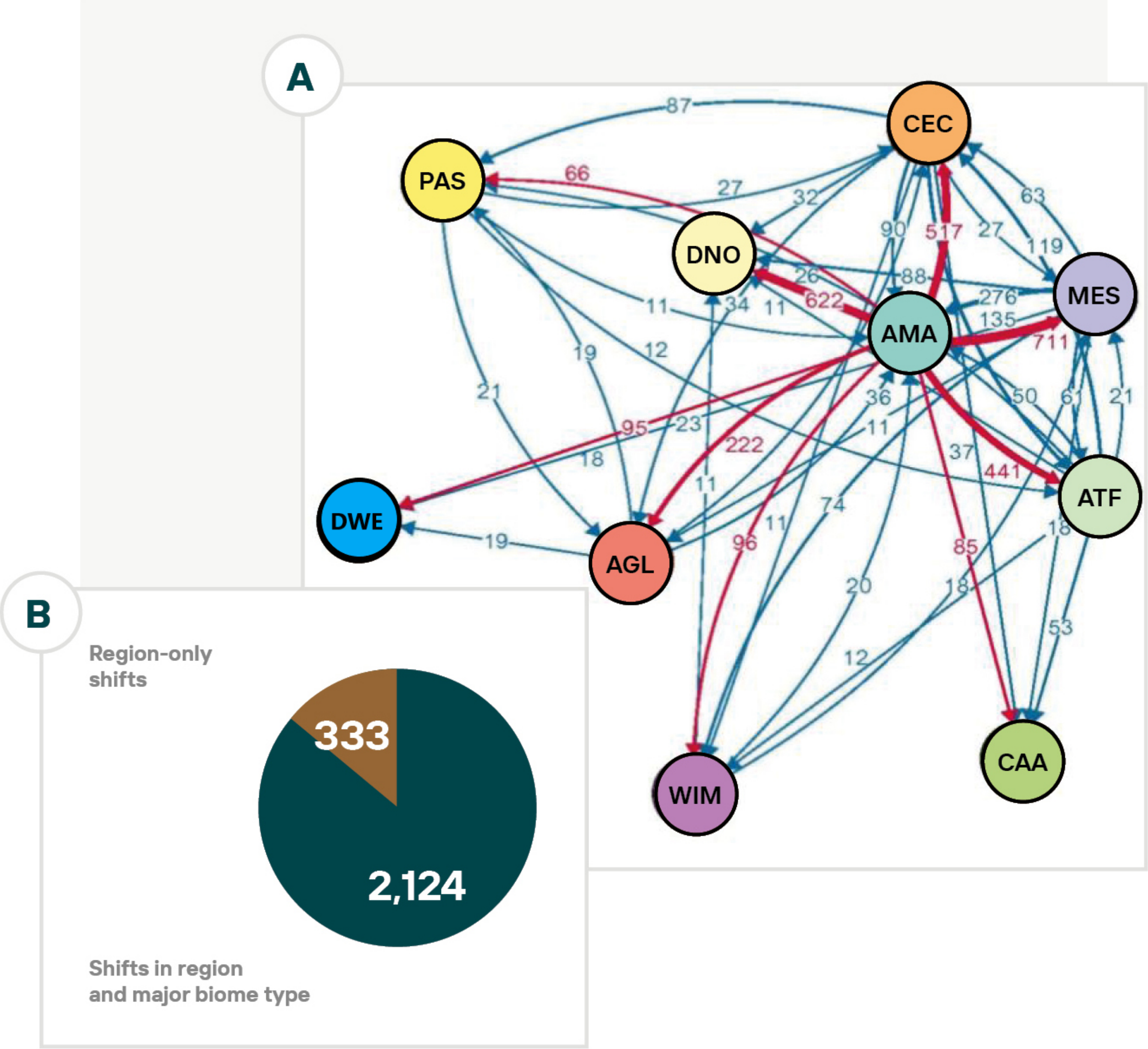

Figure 3.6 The Amazon as the main source of biodiversity lineages in the Neotropics (Antonelli *et al.* 2018b). A) Biotic interchange among Neotropical regions estimated from dated molecular phylogenies. Arrows indicate the direction and number of dispersal events, with line thickness proportional to the number of events. Only connections with more than 10 events are shown. The position of the circles in the layout reflects the biotic connection between regions. Dispersal events out of the Amazon are highlighted in red. AGL, Andean Grasslands; AMA, Amazonia; ATF, Atlantic Forests; CAA, Caatinga; CEC, Cerrado and Chaco; DNO, Dry Northern South America; DWE, Dry Western South America; MES, Mesoamerica; PAS, Patagonian Steppe; WIM, West Indies. B) Number of nonambiguous dispersal events associated with shifts in major biome types compared with shifts to other regions within the same biome type.

In the face of environmental change and impacts, populations with reduced genetic diversity may be less capable of responding (Whitman and Agrawal 2009), and thus more vulnerable to fragmentation processes and local extinctions (Spielman *et al.* 2004). This genetic diversity has been proposed as a mechanism to survive in heterogeneous or changing environments, such as the tropics (Lande 2014). A classic example regarding the constant changes in oxygen content in Amazonian waters is the development and reversal of various morphological traits in fishes under hypoxic conditions (Almeida-Val *et al.* 2006, Fernández-Osuna and Scarabotti 2016). Furthermore, the ability of various lineages to establish themselves in the western and southern Amazon may also be related to high rates of alteration and turnover in the region (Quesada *et al.* 2012, Marimon *et al.* 2013, Baker *et al.* 2014).

3.5 Functional Diversity

Functional diversity, or the value, range, and distribution of functional traits in a given community, plays a key role in the generation and maintenance of biodiversity and ecosystem processes. Functional diversity depends on the variability of trait values of all species present, both within and between species, and on the extent of overlap of functional niches (Petchy and Gaston 2006, Díaz *et al.* 2007). Functional traits (Chapin *et al.* 2001, Violle *et al.* 2007) mechanistically link species to their effect on the ecosystems in which they live. For example, functional traits affect species competitive ability and coexistence (Kraft *et al.* 2008, Guilherme *et al.* 2019), invasion ability (Miranda-Chumacero *et al.* 2012, Van Damme *et al.* 2015), community and ecosystem structure and function (Bueno *et al.* 2013, Sobral *et al.* 2017), adaptations along environmental gradients (Asner *et al.* 2014a, von May *et al.* 2017, Santos *et al.* 2019), and resistance to disturbance and environmental change (Arévalo-Sandi *et al.* 2018, Arantes *et al.* 2019, Hooper and Ashton 2020).

Environmental conditions act as filters, determining functional diversity patterns in the Amazon Basin, selecting species exhibiting similar morphological, behavioral, or reproductive traits. For example, structurally, less complex environments (*e.g.,* savannah) harbor more species of smaller ants, with smaller mandibles and larger eyes. In more complex forested environments, there are more ant species of larger size, with larger mandibles and smaller eyes. Thus, the morphological composition of ground-dwelling ant assemblages corresponds to environmental complexity, suggesting that certain ant characteristics offer ecological advantages to particular species in particular habitats (Guilherme *et al.* 2019). Tree foliar chemistry provides another example of functional diversity varying with environmental conditions. Structural and defense compounds display striking diversity in the Amazon, and chemical portfolios of tree canopies dramatically shift along elevation and soil fertility gradients (Asner *et al.* 2014b). Likewise, the diversity of functional traits in fish communities, such as feeding strategies, life histories, migratory behaviors, and habitat use, is positively correlated with forest cover in river floodplains (Arantes *et al.* 2019). Accordingly, the environment influences functional diversity, and as habitat loss from deforestation proceeds, the suite of functional traits found in fish communities is highly compromised.

The Amazon is among the most functionally diverse regions on Earth for a number of taxa (*e.g.,* fish: Toussaint *et al.* 2016; plants: Wieczynski *et al.* 2019; amphibians: Ochoa-Ochoa *et al.* 2019). 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 from taxonomic diversity. Freshwater fish represent one striking example (Toussaint *et al.* 2016), and different hypotheses have been advanced to explain the tremendous functional diversity of freshwater fishes throughout the Neotropics (Albert *et al.* 2020). The Neotropics host approximately 40% of the world's freshwater fish species, yet this same region hosts more than 75% of fish functional diversity. Freshwater functional diversity in Amazon includes incredible variation in body form and trophic ecology, ranging from suckermouth wood-eating catfish (*e.g., Cochliodon*, *Panaque* spp) with teeth and jawbones specialized for gouging submerged tree trunks, to electric fish with smaller eyes living in turbid waters (Gymnotiformes), to migratory frugivores with molar-like teeth that can be important seed predators as well as seed dispersal agents (*e.g. Colossoma, Piaractus*; Correa *et al.* 2015a), to elongated vampire catfish that feed on blood in the gills of other fishes, *Vandellia* (Albert *et al.* 2020).

Functional diversity explains biological interactions and how organisms can drive crucial ecosystem processes. For example, trophic diversity, an important functional trait, influences how species can influence ecological processes such as predator-prey interactions, seed dispersal, carbon sequestration, and biogeochemical cycling, all critical functions in Amazon aquatic and terrestrial ecosystems. Moreover, species diversity per se can be a strong driver of ecosystem function. For example, in the mixed forest-savanna landscapes of the Rupununi region of Guyana, mammal species richness appears to be strongly correlated with carbon cycling (Sobral *et al.* 2017). Interestingly, concentrations of soil carbon and carbon storage in soil and trees are highest at sites with the highest mammal species richness. Thus, the number of feeding interactions influences the amount of carbon that remains in soils, as animal bodies, feces, and fruits processed by mammals all become sources of soil organic matter. Likewise, in tropical aquatic systems, consumer-mediated nutrient recycling by fish varies greatly with traits such as consumer body size, body stoichiometry, and trophic position. Fish can modulate nutrient cycling in tropical streams (Taylor *et al.* 2006, Capps *et al.* 2013), and fish extinctions can have profound consequences on rates of nitrogen and phosphorus remineralization (McIntyre *et al.* 2007).

Functional diversity can further contribute to community and ecosystem resilience to perturbation, including climate change or defaunation. For example, plant traits such as the ability to withstand water and temperature stress can determine how composition dynamics, plant biomass, and carbon sequestration of Amazonian forests respond to prolonged periods of drought (Levine *et al.* 2016). 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 to climate change. Thus, scientists forecasting climate change impacts on Amazonian forest composition, biomass, and carbon sink function over the next century cannot neglect trait diversity (Sakschewski *et al.* 2016). Functional redundancy posits that in biodiversity-rich ecosystems like the Amazon, the extinction of some species will not cause a substantial loss in ecosystem function if remnant species play equivalent roles and are capable of taking over the functions played by extinct species (Lawton and Brown 1993). Indeed, evaluations of seed dispersal networks in Amazonian forests show high connectivity and diet overlap among several species and groups of vertebrates, suggesting high redundancy. However, observations show that fragmented and defaunated forests suffer greatly from trophic cascading effects, suggesting complementarity rather than redundancy in large vertebrates (Bueno *et al.* 2013, Arévalo-Sandi *et al.* 2018).

3.6 Incomplete Knowledge of Biodiversity

Even though the Amazon is one of the largest and most intact forests in the world, it is also one of the least known biologically. Its immense size, diversity, and limited access make the task of documenting its biodiversity extremely challenging. Consequently, there are both spatial and taxonomic biases in the data, sometimes severe (Oliveira *et al.* 2016, Schulman *et al.* 2007, Vale and Jenkins 2012). Looking at species locality data in global databases (Figure 3.7), there is a strong spatial bias towards urban areas, research centers, and major access routes (*e.g.*, roads, rivers). At the same time, some parts of the Basin have few or even no data for any taxa, or at least no data that are digitally accessible.

Looking across taxa, there are also strong biases. Most of the data available are for plants or birds (>80% in GBIF). Groups such as butterflies have far fewer data, and hugely diverse groups like fungi and bacteria are almost entirely unknown. Of course, such taxonomic biases are not unique to the Amazon; they exist for most areas of the world, a consequence of society having more interest in some taxa than others. There are also substantial numbers of still undescribed species, even for well-known taxa (Pimm *et al.* 2010). These species are also unlikely to be like ones already known. Yet-to-be-discovered species are certainly rarer

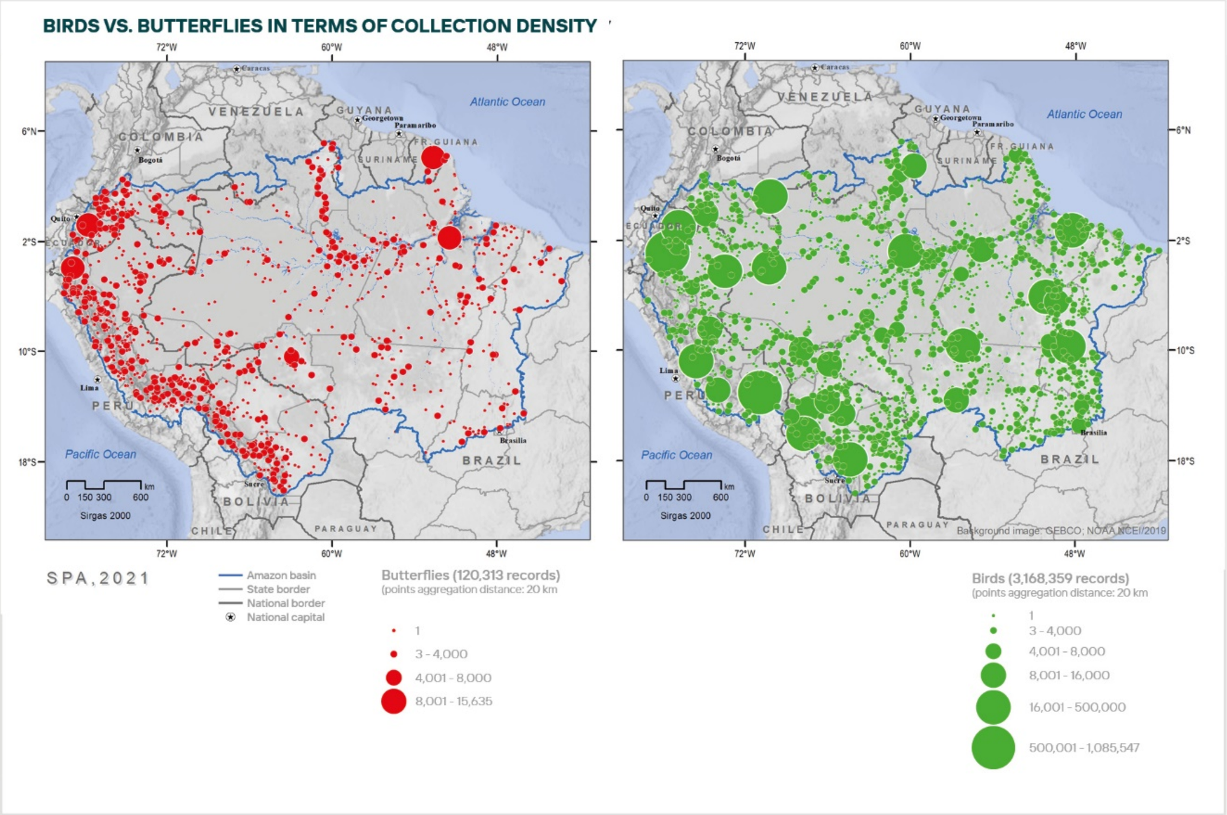

Figure 3.7 Butterflies (120,313 records) versus birds (3,168,359 records) in terms of collection density. Source: GBIF 2021. Data clustering method: Natural Jenks, Aggregation distance: 20 km.

and more restricted in their distributions than already known species. In general, it is the common and widespread species that are described first (Pimm and Jenkins 2019). Consequently, the biodiversity we do not yet know may not follow the same patterns as the biodiversity we do know today.

These spatial and taxonomic biases in the data, and our general lack of adequate data overall, affect our capacity to understand the true patterns of biodiversity in the Amazon. This includes questions such as precisely where centers of endemism are and where one might find the most endangered species, matters of great concern for conservation. Nevertheless, while such limitations in our knowledge are problematic, the reality is that all places have incomplete data. We must make decisions using the best information available, recognizing that as we learn more, it may be wise to improve upon past decisions.

3.7 Conclusions

The Amazon is a global icon of biodiversity. Still, in many taxonomic groups, species diversity is notoriously undescribed, and in-depth taxonomic studies reveal extensive cryptic diversity. As a result, estimating species richness in the region is a challenging task. Biodiversity patterns display considerable variation within the Amazon Basin, with some groups being more diverse in lowland rainforests and others in Andean environments. We are still learning about the fascinating diversity of Amazonian fauna, flora, and fungi, and this knowledge is critical for the conservation of the Amazon region.

Plant-animal and trophic interactions are central ecological processes in Amazonian forests, without which these forests would cease to exist. These networks of mutualists and consumers regulate all aspects of Amazonian forests, and are responsible for their composition, species regulation, recovery from disturbance, and the generation of biodiversity. Changes to species interactions can have cascading effects on Amazonian ecosystem function and the services they provide humanity. An overwhelming and central result from the study of Amazonian forests is that intact plant-animal interaction networks are essential for the resilience of forest biodiversity to anthropogenic change, and for the recovery and restoration of Amazonian systems.

Aquatic ecosystems in the Amazon are a complex mosaic of habitats influenced by flood pulses and by the pattern of nutrient flow. The juxtaposition of low and high productivity waters promotes complex adaptation processes among native organisms. Migratory fish play important ecological roles in Amazonian aquatic food webs, transferring energy and nutrients among different components of the ecosystem, either as predators, prey, engineer species, or seed dispersal agents. Modification or disruption of their migratory patterns by overharvesting, impoundment, or habitat degradation alters ecosystem processes and trophic cascades, primary production, detrital processing, and subsidies transfer over wide spatial scales.

Both inter- and intra-specific variation in functional traits in Amazon biota is enormous. Functional diversity determines species competitive ability and coexistence, diversification, invasion ability, community and ecosystem structure and function, adaptations along environmental gradients, and resistance to disturbance and environmental change. Functional diversity, for example, can further contribute to community and ecosystem resilience to perturbations, including climate change. Therefore, scientists forecasting climate change impacts on Amazonian forest composition, biomass, and carbon sink function over the next century cannot neglect trait diversity.

Existing spatial and taxonomic biases in biodiversity data in the Amazon affect our capacity to understand the true patterns of biodiversity in the region. These gaps include questions such as the location of centers of endemism, areas with the most endangered species, and other questions of great concern for conservation. Although such knowledge gaps may be problematic, they should not prevent decision-making informed by current knowledge and open to incorporating novel information as it becomes available. Public policies are of extreme importance for supporting biodiversity-based basic and applied research in the Amazon, involving transnational and diverse research teams.

3.8 Recommendations

- Promote field-based, laboratory, and collection-based herbarium/museum studies and research collaborations that seek to compile a comprehensive catalog of Amazonian species, complemented with properly preserved vouchers and their tissues/DNA extracts (for molecular studies).
- Support taxonomy, currently an underfunded and underappreciated discipline. We need more taxonomists working alongside molecular biologists and local people willing to contribute their wealth of traditional knowledge towards the description of new species.

Box 3.2 Trends in the Discovery of New Species of Vertebrates in the Amazon Basin

Each year, new species of vertebrates from the Amazon are described, a process of discovery that began several centuries ago. The first Amazonian vertebrates were described by Linnaeus in 1758: 13 fish, 10 amphibians, 50 reptiles, 131 birds, and 51 mammals. To analyze trends in the descriptions of Amazonian species, 2,406 species of fish were taken as reference (Jézéquel *et al.* 2020), 997 species of amphibians (GBIF: 10.15468/dl.9mgq7k), 804 reptiles (GBIF: 10.15468/dl.uy6mw9), 2,736 birds (GBIF: 10.15468/dl.3zkc3v), and 974 mammals (GBIF: 10.15468/dl.ttgkq4), for a total of 7,827 species (Figure B3.2.1). This exercise does not aim to determine the total number of species in the Amazon, but rather to describe trends in the rate of species descriptions.

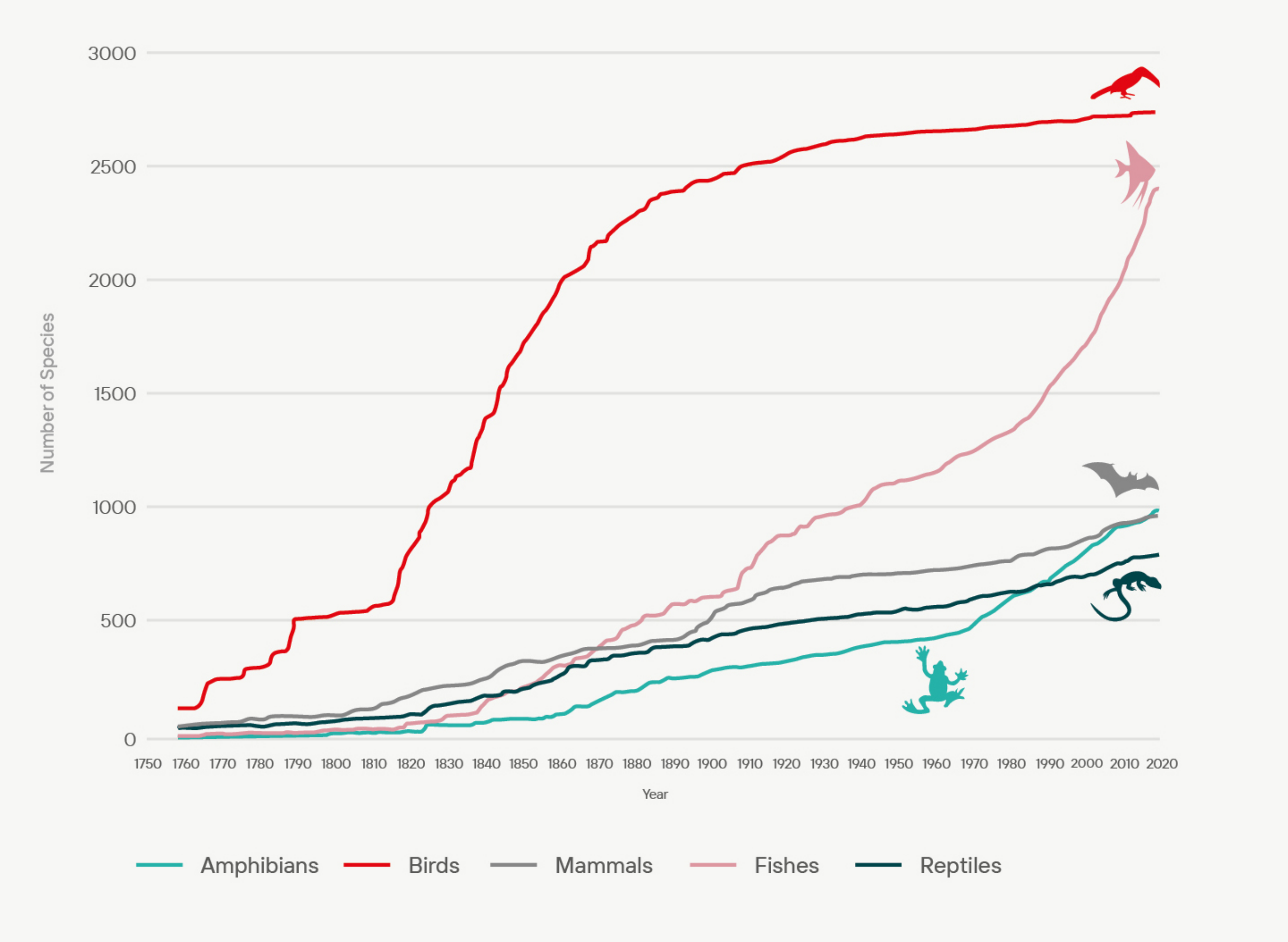

Figure B3.2.1 Species accumulation curves for five vertebrate groups from the Amazon Basin.

Fish After the first species descriptions made by Linnaeus, there was a period with a very low rate of descriptions until 1830. Starting with contributions from naturalists such as Achille Valenciennes (1794–1865) and Johann Jakob Heckel (1790–1857), there was a sustained increase until the beginning of the 20th century. Around 1910, with the main contributions of Franz Steindachner (1834–1919) and Carl H. Eigenmann (1863–1927), there was a significant increase from approximately 600 species to just over 1,000. Between 1940 and 1980 there was a constant increase, but it is remarkable that, since then, when the number of species was at 1,355, there has been a sustained exponential increase in the number described. Indeed, between 2010 and 2020, the largest number (n=412) and proportion (17%) of species were described of any decade (Figure B3.2.2). Between 1980 and 2019, 44.3% of the Amazon species were described.

Since 2016, a rate equivalent to one new species every week has been reached. This is also reflected by the historical peak of descriptions reached in the last decade with a total of 412 species (Figure B3.2.1). According to Jézéquel *et al.* (2019), the Amazon Fish database (https://amazon-fish.com) recognizes 2,406 valid species (Jéjéquel *et al.* 2019), with a clear tendency to continue adding new ones. In time, fish may become the vertebrate group with the highest number of species in the Amazon.

Amphibians The rate of descriptions of new amphibians was very low until 1860, when it increased and remained relatively constant until 1970 (Figure B3.2.3). From the 1970s onward the rate dramatically increased, with 50.65% of Amazonian species described in the last 50 years.

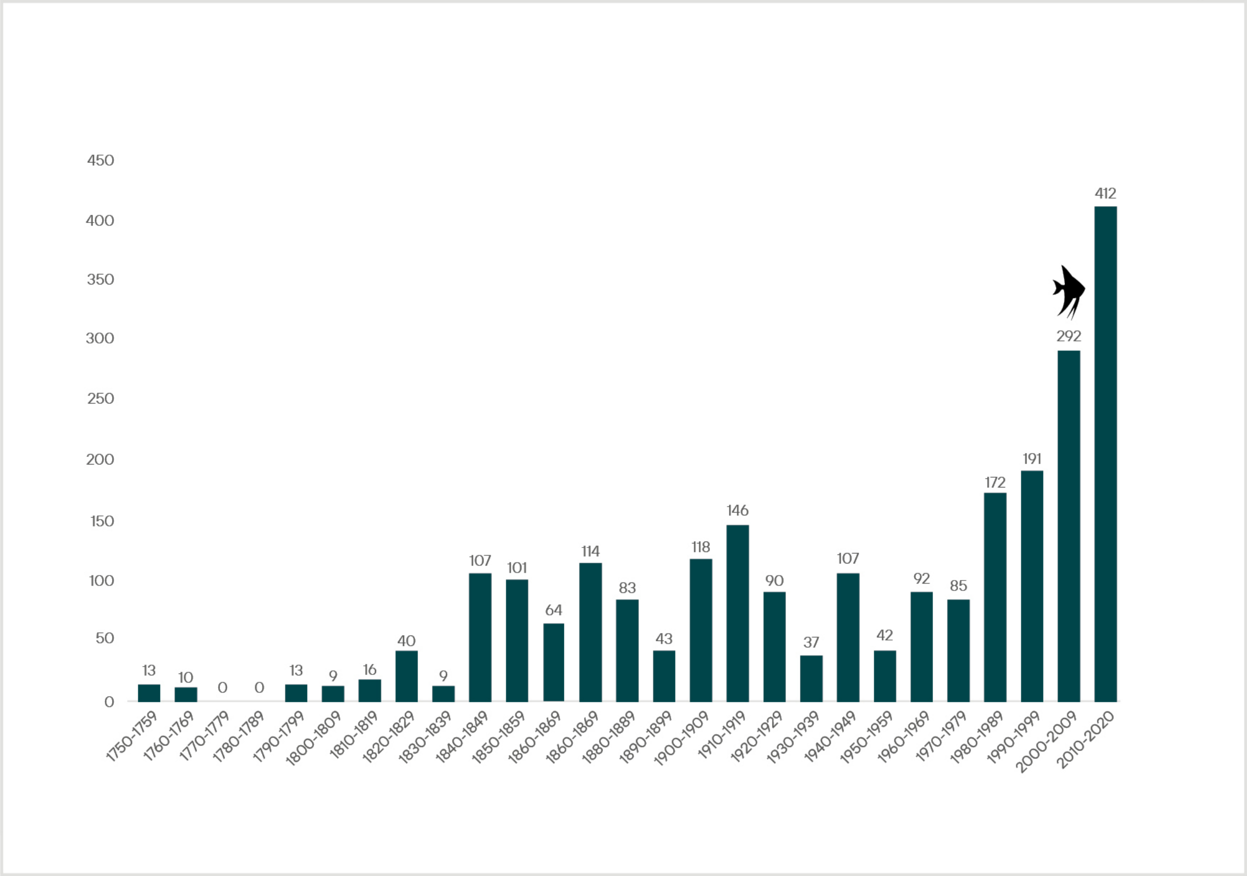

Figure B3.2.2 Number of fish species described per decade in the Amazon Basin

In the 1990s and 2000s, description peaks were reached with 128 and 118 species, respectively (Figure B3.2.3). According to the data available at the GBIF, 997 valid amphibian species have been described for the Amazon, with a tendency to continue increasing, and constituting a priority group of vertebrates for taxonomic efforts. Species discovery has benefited from the incorporation of molecular and acoustic data, as well as the increased number of herpetologists in South America.

Reptiles Since Linnaeus's initial descriptions of 50 species (1758), reptiles are the group of vertebrates with one of the lowest rates of description (Figure B3.2.1), and the lowest number of species described to date (804). Although descriptions have continuously increased, there is not a period of marked increase as with other vertebrate groups, perhaps highlighting the need for further taxonomic efforts. In the 1860s, a peak of descriptions was reached with 74 species (9%), whereas in recent decades, between 1990 and 2010, there was an increase in the number of species described, reaching a peak of 54 between 2000 and 2009 (Figure B3.2.4).

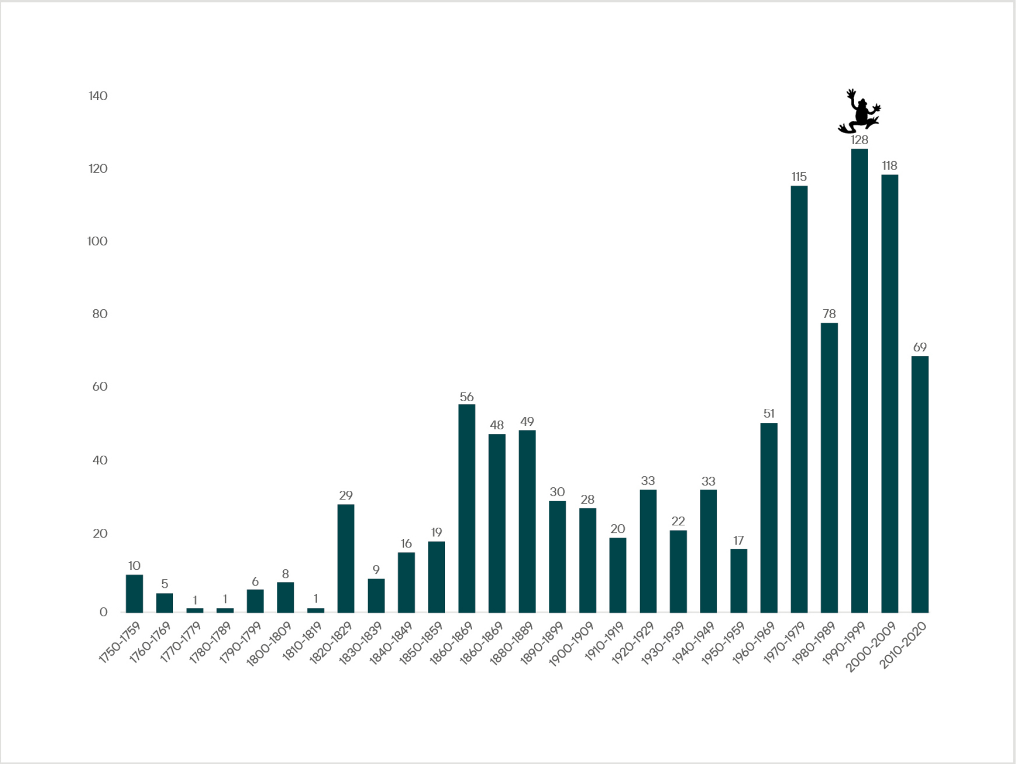

Figure B3.2.3 Number and percentage of amphibian species described by decade in the Amazon.

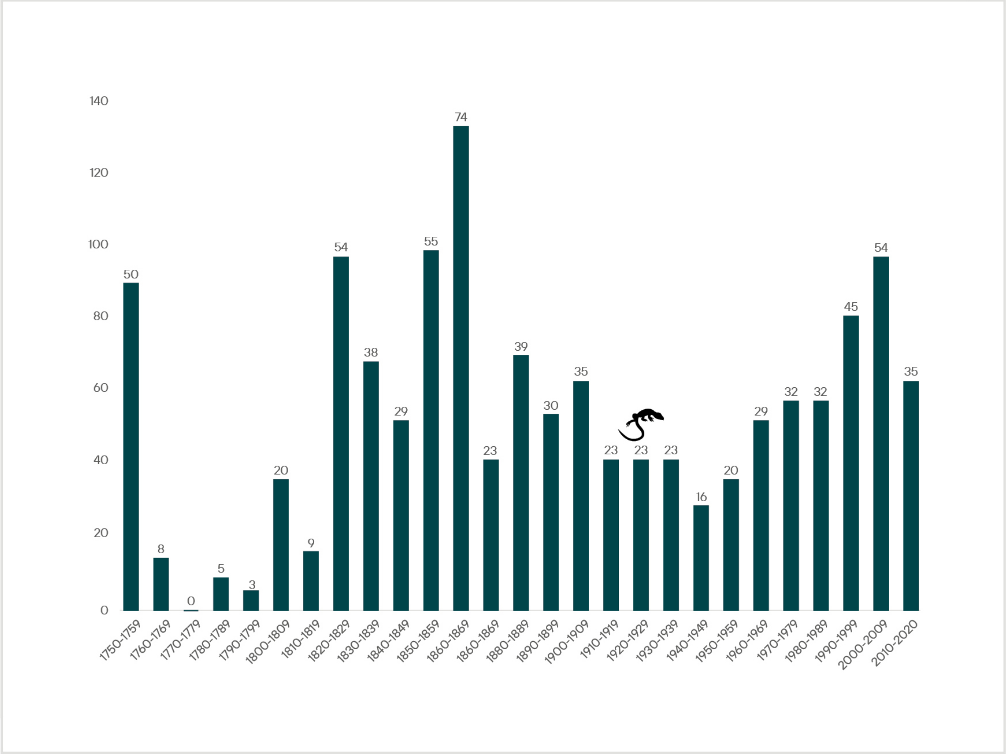

Figure B3.2.4 Number and percentage of reptile species described by decade in the Amazon.

Birds Since Linnaeus described 150 bird species, this is the vertebrate group with the largest number of species, currently with 2,736 according to GBIF data (Figure B3.2.1). Although there was very little increase between 1790 and 1810, the number of species rapidly increased to 2,500 by 1910. The peak of Amazon species descriptions occurred between 1840 and 1849, with 349 species added (17%), accounting for 58.2% of species added between 1810 and 1870 (Figure B3.2.5). Since 1910, species descriptions have significantly slowed down, with just 25 species added since the turn of the century. This trend suggests that birds are the best-known vertebrate group with the least number of species remaining to be described.

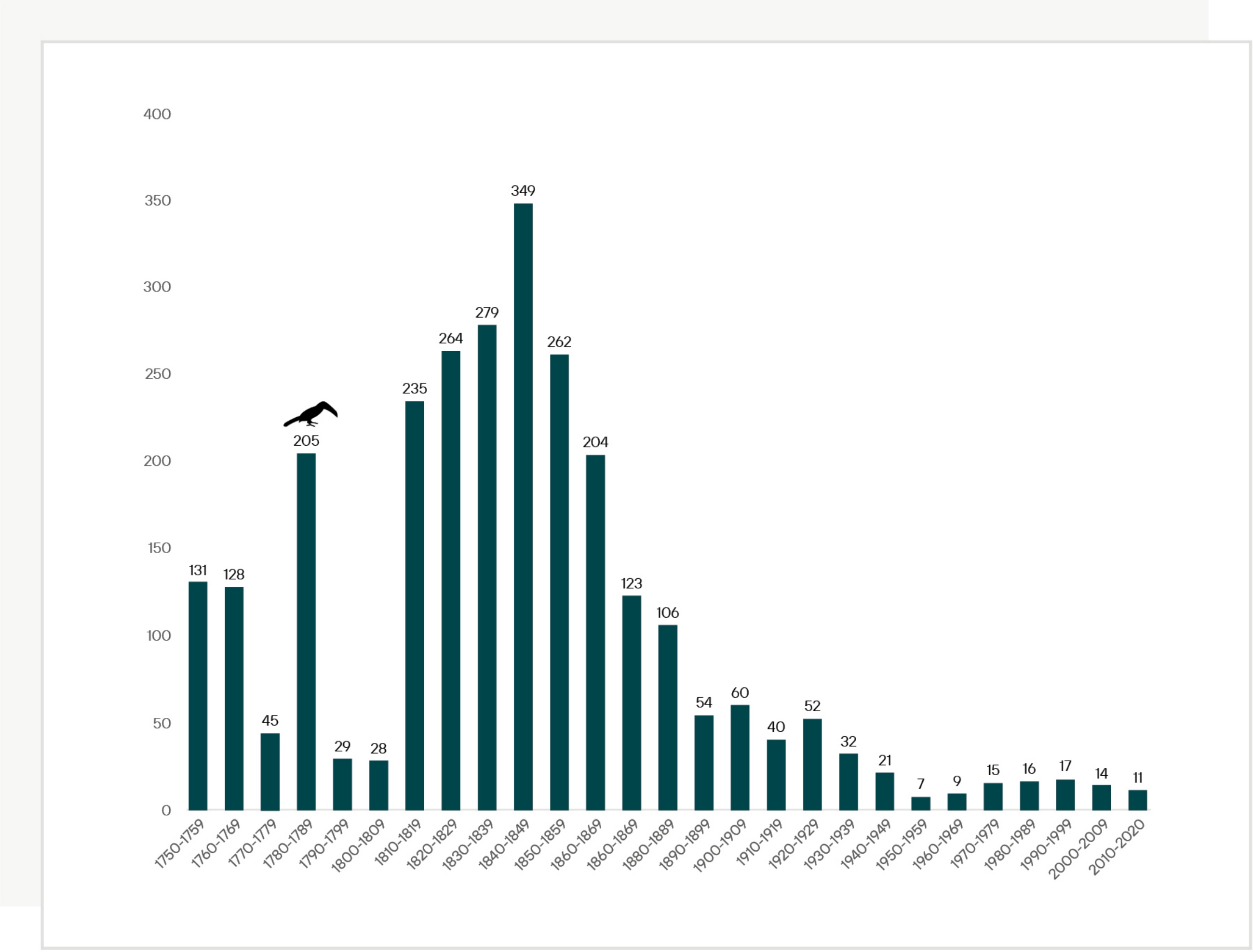

Figure B3.2.5 Number and percentage of bird species described by decade in the Amazon.

Mammals When descriptions of Amazonian mammal species began (51 species described by Linnaeus in 1758), they occupied second place, after birds (Figure B3.2.1). The number of mammal species moved to third place between 1860 and 1870, a position it held until the last decade, when amphibians overtook mammals (975 vs 997, respectively) (Figure B3.1 and Figure B3.2.6).

The rate of descriptions has remained relatively constant with increases in 1840 and 1900–1920, with the latter period being the peak in descriptions (92 species, 9%, Figure B3.2.6). The greatest potential for further new mammal species in the Amazon are among bats, rodents, and marsupials.

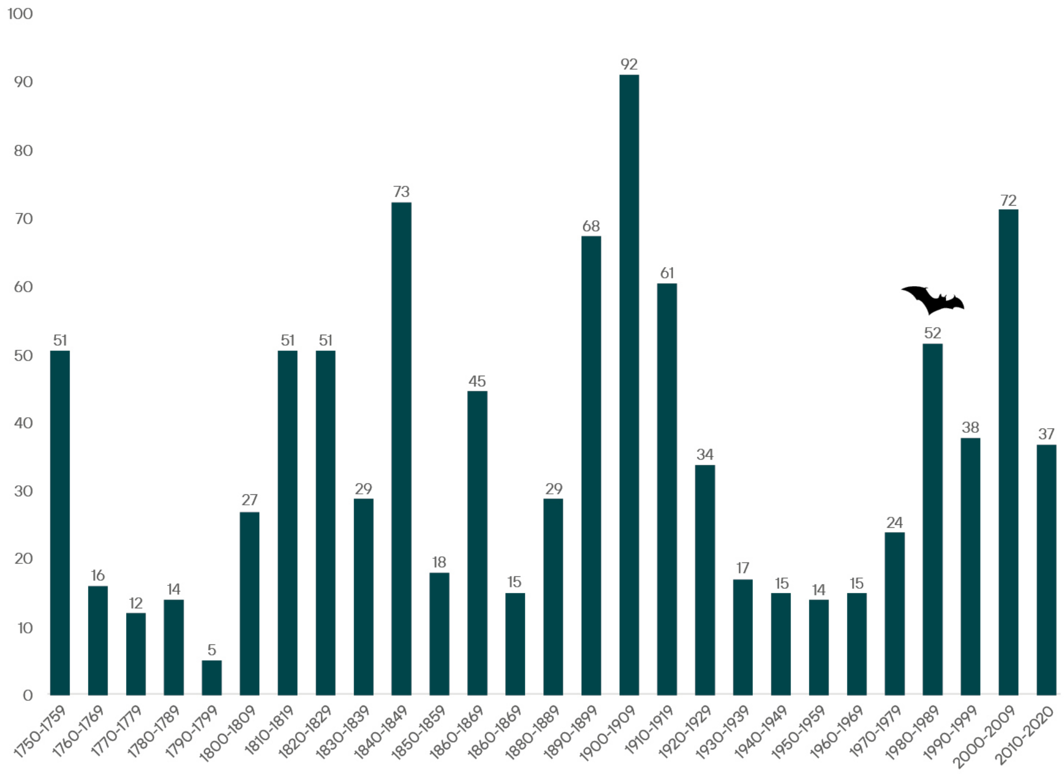

Figure B3.2.6 Number and percentage of mammal species described by decade in the Amazon.

Patterns of discovery vary widely among vertebrate classes in the Amazon, and the rates of new species descriptions, for each decade, have been highly variable between groups. To continue with the high rates of new species descriptions, particular attention should be given to the formation of integrative taxonomists, especially for fish, amphibians, and small mammals, whose species accumulation curves are far from reaching an asymptote, as happens in birds. New species are being continually described in the Amazon, including areas affected by the negative impacts of human activities. Efforts to describe new species before they are lost to habitat destruction must be intensified if we want to know the true levels of species richness in the Amazon, and the most effective ways to preserve it.

Methodological note: Species lists with the year of description for each species were used in the analysis. In the case of fish, the list available from Amazon Fish (Jézéquel *et al.* 2020) was used, while for the rest of the groups the species lists were extracted from the GBIF, using a polygon that covers the entire Amazon basin (Amphibians, DOI: 10.15468/dl.9mgq7k; reptiles, DOI: 10.15468/dl.uy6mw9; birds, DOI: 10.15468/dl.3zkc3v; and mammals, DOI: 10.15468/dl.ttgkq4). In all cases, it is assumed that GBIF and Amazon fish lists have the taxonomic information reviewed and validated. Only the scientific names that include author and year were used, so the species totals do not necessarily indicate the total number of species present in the Amazon. The polygon drawn for the GBIF download may have omitted some species or included species that do not necessarily occur in the Amazon.

- It is crucial to maintain altitudinal connectivity from the Amazon to the Andes. Otherwise, species will lose the ability to migrate in response to climate change.

It is essential to establish large-scale, landscape-level, conservation initiatives that maintain core areas and connectivity to secure the survival of wide-ranging species, migratory species, rare species, species with patchy distributions, and the diversity of functional traits.

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