Science Panel for the Amazon (SPA)

Working Group 2

BIODIVERSITY AND ECOLOGICAL FUNCTIONING IN THE AMAZON

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CHAPTER 3. BIOLOGICAL DIVERSITY AND ECOLOGICAL NETWORK IN THE AMAZON

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CHAPTER 3. BIOLOGICAL DIVERSITY AND ECOLOGICAL NETWORK IN THE AMAZON

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ACRONYMS AND ABBREVIATIONS

IUCN, International Union for Conservation of Nature

DD, Data deficient (IUCN category)

VU, Vulnerable (IUCN category)

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KEY MESSAGES

✔ The Amazon basin is one of the most biodiverse areas in the world for most taxonomic groups. However, diversity varies geographically, with some groups being more diverse in the Amazon lowlands, whereas others thrive in the Andes.

✔ Current evaluations underestimate the true species richness of the Amazon, partially due to the difficulty of sampling in this vast region. The Amazon presents an incredibly high rate of discovery of new species (one every other day) and, at the current rate, it will take several hundred years to compile a complete list of plants and animals (not to mention their geographic distribution, natural history, and conservation status). Further, some groups, such as fungi and bacteria, are understudied.

✔ Plant-animal interactions are a central ecological process in Amazonian forests, without which these forests would cease to exist. Such interactions have led to the evolution of high species diversity. These networks of mutualists and consumers determine all aspects of Amazonian forests and are responsible for their composition, species regulation, recovery from disturbance, and the generation of biodiversity that comprises the forest.

✔ It is essential to halt deforestation and forest fragmentation, and to establish large-scale, landscape-level restoration and conservation initiatives that maintain core areas (including terrestrial and aquatic environments, which are inter-dependent) and connectivity between areas. This is essential to securing the survival of species with large ranges, migration patterns, patchy distributions, low population numbers, and the diversity of functional traits they present.

ABSTRACT

Scientists have not estimated yet, to the nearest order of magnitude, the number of species in the Amazon. While the Amazon is one of the largest forests in the world, it is also one of the least known biologically. Documenting its biodiversity is challenging because of immense size, diversity, and limited access. On the basis of current knowledge, the Amazon exhibits the highest density of species, as well as the highest number of endangered species (many of them endemics) 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 species migrate over long distances, and some of them perform the world longest migrations known in freshwaters, using the entire length of the Amazon basin in a round trip migration of up to ~12,000 km. It is also important to consider that plant-animal interactions and trophic interactions are central ecological processes in Amazonian forests. Disruptions to these interactions can alter forest community composition over the long-term. Functional diversity, including intra- and inter-specific variation in organisms, has recently attracted attention from 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 Amazon biodiversity, species assemblages, and ecological interactions. There are spatial and taxonomic biases in the data (including many unexplored localities and lesser-known taxonomic groups) which affect our understanding of biodiversity patterns in the Amazon. The 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, flora, fauna, plant-animal interactions, migration, phylogenetic diversity, functional diversity.

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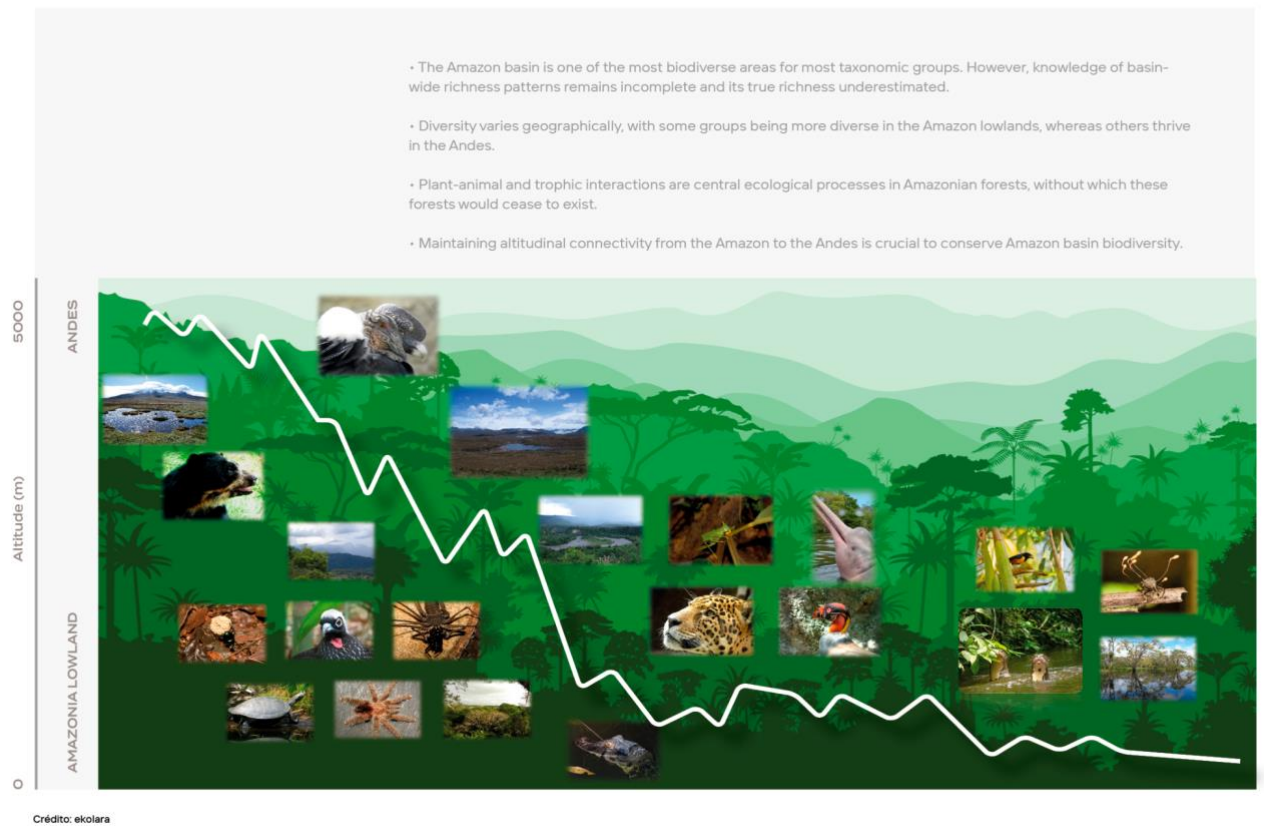
The Amazon is the most biodiverse area for most taxonomic groups. Photos show iconic species and ecosystems along the altitudinal gradient of the region, and selected species interactions. Background illustration by ekolara. Photos by Esteban Suaréz, Galo Zapata-Ríos, Fernando Trujillo, Robert Schlappal/©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

1. WHY IS THE AMAZON SO RICH IN SPECIES AND ECOSYSTEMS?

The Amazon is the most biologically diverse area on the planet. Encompassing 6.9 million square kilometres, its biodiversity is inconmensurable. 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 plant species, at least 2406 fishes in the Amazon basin, and 427 amphibians, 371 reptiles, 1300 birds, and around 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 number of species in the Amazon basin, and for some groups are biased to the Brazilian Amazon (http://censo.museu-goeldi.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 Text Box 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). 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 contributed to generate the high Amazonian biodiversity (see chapter 2 for different models of diversification). Tectonics, hydroclimate, evolutionary and ecological factors, disturbance regimes, among others (see chapter 2), and the more recent legacy of a cultural landscape (see chapter 10) are some important processes.

Biodiversity refers to the number of species, the variety and variability of living organisms (*e.g.*, plants, animals, microorganisms), including terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which they are part. Included in the concept of biodiversity are the diversity within species (genetic diversity), between species, and of ecosystems (UN Convention on Biological Diversity, Article 2). 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, like 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 in the Amazon suggest 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 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 groups, adding complexity to the analysis of environmental history and biotic diversification in the Amazon.

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 species of flooded habitats depend on the environments associated with river dynamics and the cycle of floods (the flood pulse), so their evolution is historically linked to the broad Amazon drainage system (Toews *et al.* 2016; Moraes *et al.* 2016). Historically riverine dynamics could have influenced the recent evolution and distribution of species adapted to flooded environments and possibly interrupted the movement between eastern and western populations of the Amazon, as suggested by phenotypic variation in vertebrates and confirmed by genomic analysis (*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 the species 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, the pulse and fluctuation of seasonal floods in the great alluvial river plains of the Amazon, complemented by macro-regional climatic events (Junk 1997).

The purpose of this chapter is to provide an overview of the biodiversity levels in the Amazon region, why this region is so rich in species and ecosystems, and outline some outstanding ecological processes that make the Amazon an icon of the natural world. A

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group of selected terrestrial and aquatic taxonomic groups have been included to exhibit how much we know about diversity levels in the Amazon, and more importantly how much we still do not know, and yet 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.

2. BIOLOGICAL DIVERSITY PATTERNS OF SELECTED TAXONOMIC GROUPS

2.1. Vascular plants

Intangible oral transmission perpetuated traditional knowledge, agricultural practices, traditional medicine, or food preparations of Amazonian plants from generation to generation. Pictorial depictions in artifacts (*e.g.* in 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. The first Europeans chronicled and illustrated domesticated plants, such as chili pepper, cassava, 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 is 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 18th century with the goal to discover and document medicinal plants, such as quinine (cascarilla bark, *Cinchona officinalis*; Ruiz 1792; Ruiz and Pavón 1801). These early expeditions, alongs with and 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 19th 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 in1866, Georgetown University in 1879, Rio de Janeiro Botanical Garden in 1890), followed by many others at the turn of the 20th century. During the second half

of the 20th 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 and new species of plants described to science, and an array of floristic 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 were published for each country (BFG 2018; Ulloa Ulloa et al., 2017; Ulloa Ulloa and Jørgensen 2018; Table 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 1).

Table 1. Native vascular plant (all plants) diversity in Amazonian countries and references.

Country/region	Guiana Shield	Colombia	Ecuador	Peru	Bolivia	Brazil
Total vascular plants (Ulloa Ulloa et al. 2020 or specified)	8,384 / 13,249 (Funk et al. 2007a)	24,020	18,463	19,809	14,733	34,459 (BFG 2018)
Below 1000 m, seed plants	6,890	5,835 (Bernal et al. 2015)	3,607	5,401	3,518	11,846
(Cardoso et al. 2017 or specified)						(BFG 2018)
Ongoing country flora	Flora of the Guianas (Görts-van Rijn and collaborators 1985–present)**,** Flora of the Venezuelan Guayana	Flora de Colombia (1983–present)	*Flora of Ecuador* (Sparre et al. editors, 1968–present).	*Flora of Peru* (MacBride and collaborators 1936–present,	In preparation (see Meneses et al. 2015)	Flora do Brasil 2020 online

	(Steyermark et al. 1995–2005)			see Gentry, 1980)		
Catalogue of plants ref.	Funk et al 2007a; Feuillet 2009	Bernal et al. 2015	Jørgensen and León-Yánez 1999; Neill and Ulloa Ulloa 2005;Ulloa Ulloa and Neill 2005	Brako and Zarucchi 1993; Ulloa Ulloa et al. 2004	Jørgensen et al. 2014	Forzza et al 2010, BFG 2018,
Red List Endemics		Ongoing (Calderón et al. (2002–present, not exclusive to endemic	León-Yánez et al. 2011	León et al. 2006 [2007]	Ongoing (Navarro et al. 2012–present)	Martins et al. 2018

Useful/medicinal plants		Pérez Arbelaez 1956, 1990.	Acosta Solis 1992; De La Torre et al.; Ríos et al.			See Dutra et al. 2016; Vieira et al. 2016; Coradin et al. 2018
Regional	Correa Q. 1989; National Research Council, 1989 ; Tejedor Garavito et al. 2012					

A recent compilation of the 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 that correspond to 20% of all of the world's plants (Ulloa Ulloa *et al.* 2017, 2020; Nic Lughada *et al.* 2016, Table 1). Aproximately 4% 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 1**, **Figure 1**). There is not an authoritative list for all of vascular plants of the Amazon basin, but estimates for seed plants occurring below 1000 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 flora varies between 6,727 to16,000 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 yet imperfect knowledge of richness for Amazonian plants.

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BOX 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). At the time of the European contact, over a 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, as well as numerous fruit trees and 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). A few species, however, still have high importance in the region (Alexiades and Shanley 2004; Shanley *et al.* 2011). The Andes region provided the world with the potato (*Solanum tuberosum* complex), the tomato (*Solanum esculentum*), bell pepper and *ajíes* (*Capsicum* spp.), and beans (*Physallis* species) selected and manipulated genetically 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 in communal properties, peasants overexploit their resources (Balslev et al. 2015). The majority of native palms from the tropical Andes from Colombia to Bolivia (67% of the 336 species) is a source for different uses and applications like in food, construction materials, oils, among others (Valencia et al. 2013; Moraes et al. 2015). While exploring Venezuela, Humboldt and Bonpland (1805) collected and described to science the Brazil nut, as *Bertholletia excelsa* (Lecythidaceae), a species of tree already well known by its inhabitants long before the arrival of European explorers, and widely spread in lowland Amazonia. Recent analyses of tree species composition of lowland Amazonian forests revealed the "hyperdominance" of a few species; many domesticated such as the Brazil nut and various palm species, indicate that modern tree communities in lowland Amazonia 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 5300 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- 2200 m asl (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, known for the best fiber quality (Liu *et al.* 2015). Important crops likely originating in southwestern Amazonia are manioc (*Manihot esculenta*), peach palm (*Bactris gasipaes*), and peanuts (*Arachis hypogea*) (Clement et al., 2016). The most important medicine coming out 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 produced synthetically and found in the bitter flavor of tonic water (Ulloa Ulloa, 2016 [2007]). The coca plant (*Erythroxylum coca*) grows on the 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.

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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 of plants of Ecuador (León-Yánez *et al.* 2011), Peru (León *et al.* 2006 [2007]), and Brazil (Martins *et al.* 2018). Sixty-five percent of the endemic species evaluated (8564) are threatened, i.e. in the IUCN categories Critically Endangered (CR), Endangered (EN) or Vulnerable (VU) with a perceived high risk of extinction (**Figure 2**). This percentage is well above the worldwide estimated risk for tropical countries of 47% (Pitman and Jørgensen 2002). In addition, 2011 endemic species were "Data Deficient (DD)" (*i.e.*, without enough information for an assessment), which could underestimate the number of threatened species. Poorly known species could go extinct without even being reported (Humphreys *et al.* 2019). The endemic plant species evaluated from Ecuador, Peru and Brazils (13,165 species) represent combined about 19% of the total of endemic species (*ca.* 67,900) from tropical South America (Ulloa Ulloa *et al.* 2017, **Figure 2**). For Ecuador alone, a worrisome 78% of endemic plant species are under some risk of threat due to deforestation or habitat alteration (León-Yánez *et al.* 2011). Although national Red

Lists and Data Books may be imperfect or preliminary assessments, they give at present an overview of the conservation situation and provide a basis for conservation actions (Pitman and Jørgensen 2002).

Figure 1. Number of vascular plants (all plants) in Amazonian countries. For each area, the total number of species of native vascular plantsand the number of endemic species (in parenthesis) to that area are indicated (Data from Ulloa Ulloa *et al.* 2020. Illustration by C. Ulloa Ulloa).
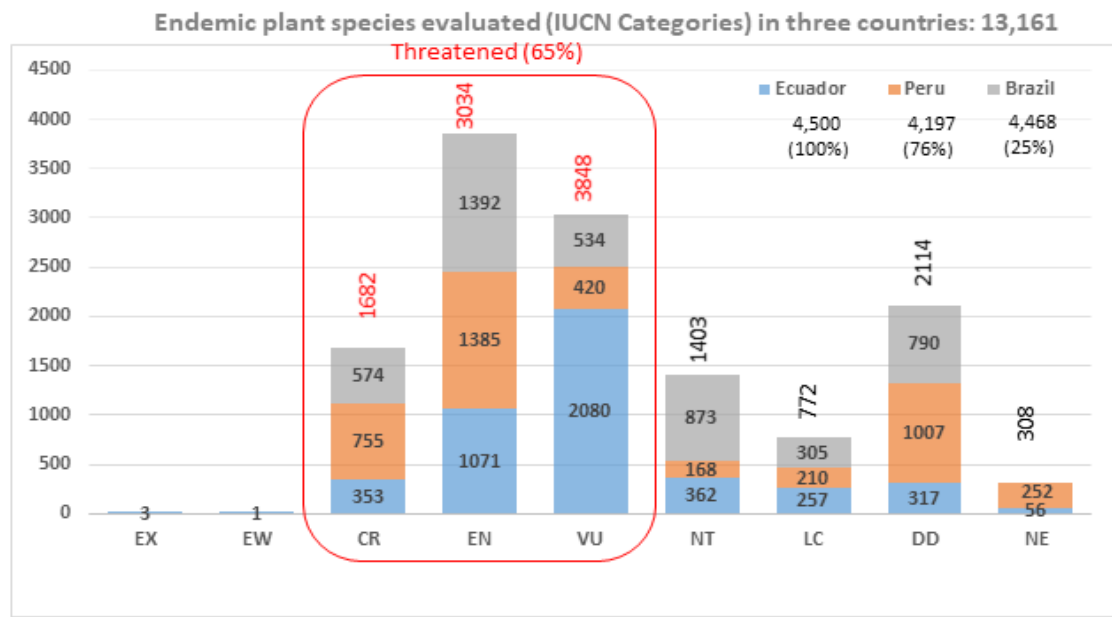
Figure 2. Plant endemics (all plants) of Brazil, Peru, and Ecuador evaluated with IUCN conservation status categories. The red rectangle encloses the three threatened IUCN Red List categories. IUCN categories: EX=Extinct; EW=Extinct in the Wild; CR=Critically Endangered; EN=Endangered; VU=Vulnerable; NT=Not Threatened; LC=Least Concern; DD=Data Deficient; NE=Not Evaluated. Number of endemic plant species evaluated: Ecuador 4500 (100% of endemics, León-Yánez *et al.* 2011); Peru 4197 (76%, León *et al.* 2006 [2007]); Brazil 4468 (25%, Martins *et al.* 2018).

2.2. Fungi and non-vascular plants

Also called cryptogams, the non-vascular plants group includes algae, lichens, bryophytes, and fungi, and they are the main drivers of the carbon and nutrient cycle and hydrology at high latitudes (Beringer *et al.* 2001, Lang *et al.* 2009). Biogeographically, it is the striking difference in the abundance of non-vascular plants in the Amazonia compared to mountain forests. As vascular plants, non-vascular plants have their center of diversity in the Tropical Andes, although there, species diversity is positively related to altitude. Often overlooked in these habitats, the total diversity of these taxa is typically underestimated (Ferris *et al.* 1996). There are a large number of species of algae and, although the bibliographic references differ greatly 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, are different organisms from plants and animals because they excrete digestive enzymes and absorb externally digested nutrients. Although the factors that determine its diversity remain little explored, estimates of the number of species for the planet vary from 500,000 to almost 10 million. Recent studies have suggested that fungal diversity is greater in the tropics than in subtropical mountainous areas (Arnold and Lutzoni, 2007; Tedersoo *et al.*, 2014), the fact is that these areas have been studied considerably less (Barnes *et al.* 2016). Lichens are organisms composed of two symbiotic organisms: 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 the 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 for 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 Amazonia with 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 favor the growth of this group of plants (Chaverri-Polini 1998).

2.3. Diversity of insects

Although insects dominate terrestrial ecosystems (either measured by number of species or total biomass), the number of terrestrial insects in the Amazon region is unknown (Adis 2007; Hanson and Nishida 2016). Amazonian entomofauna is amazingly rich all along the different vertical forest strata, and it would be expected that the patterns of distribution of species at large spatial scales are not evenly distributed 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, ants and mosquitoes (Formicidae and Diptera) 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. However, available data (*e.g.* Erwin 1998; Adis 2007) suggest that some groups originated in the Neotropics and are widely distributed beyond the borders of Amazonia (*e.g.* leafcutter ants, *Atta* spp.); other groups originated along the Andes or the Guyana shield, with a subsequent dispersal into the Amazon Basin (*e.g.* Meinertellidae); while 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 is 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 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 water quality efforts (*e.g.* Heckman 2011; Hamada *et al.* 2014).

Many studies of Amazonian aquatic insects have examined water quality, because of the insects's 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 knowledge 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 hold half of the known aquatic insects, notably Chironomidae (Trivinho-Strixino 2019). Several taxa are considered aquatic bioindicators due to the dependence of at least at some stage of life to the aquatic environment. 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). Amazonian aquatic insects are still partially known, and elaborating necessary species list requires a gigantic effort. When updating the list of Trichoptera, Paprocki and França (2014) found an increase of more than 65% in the number of species, where 90% 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 continuous increase in the rate of description of new species can reduce this knowledge gap (Rafael *et al.* 2009).

2.4. Diversity of fish

The Amazon basin contains the world's most diverse freshwater-strict fish fauna, with 2406 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 (1402 endemic species, Jézéquel *et al.* 2020). Part of this diversity also includes marine taxa that have adapted to freshwaters, 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 the contemporary Amazon 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 a recent establishment of the modern Amazon River (~ the last 2.5 Ma ago), 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 the Amazon 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 low oxygen concentrations found in floodplains), trophic habits (blood sucking, scale eating, the Arahuana jumping several meters outside the water to feed on insects, spiders, birds or reptiles on tree branches, etc.) reproductive adaptations (*e.g. Copeina arnoldi*, that jump outside of the water to 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 (*Osteoglossum* spp., Moreau and Coomes 2006). By contrast, medium-sized and large species (belonging mostly to the Order Characiform and Siluriform, but also Perciform, Cichliform, Clupeiform, or Osteoglossiform) support important fisheries throughout the basin and serve as an economic sustenance and as a main source of animal protein for many of the inhabitants of the Amazon basin (Barthem and Goulding 2007; Duponchelle *et al.*, 2021).

2.5. Diversity of amphibians

Amphibians are an ecologically and behaviorally diverse group of vertebrates containing 8300 species that range from the familiar frogs, toads, and salamanders, to the fossorial caecilians (Duellman and Trueb 1986, Wells 2013) (**Figure 3**). Out of the 8300+ species of amphibians known to exist today (Frost 2020), the Amazon basin exhibits the highest density of species, and the highest number of endangered species (*AmphibiaWeb* 2020, Bass *et al.* 2010, Scheele *et al.* 2019) (**Figures 4** and **Figure 5**).

Figure 3. Amphibian diversity in the Amazon basin. (A) Embryos of the Andean glassfrog *Nymphargus wileyi*. (B) Torrent frog, *Hyloscirtus staufferorum*. (C) Tiger-stripeed Monkey Frog, *Callimedusa tomopterna*. (D) Amazonian salamander, *Bolitoglossa* sp. Photos by Tropical Herping.
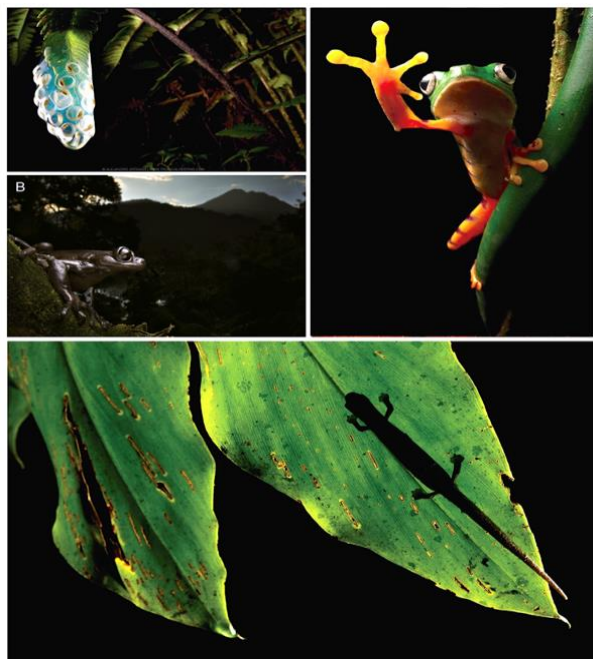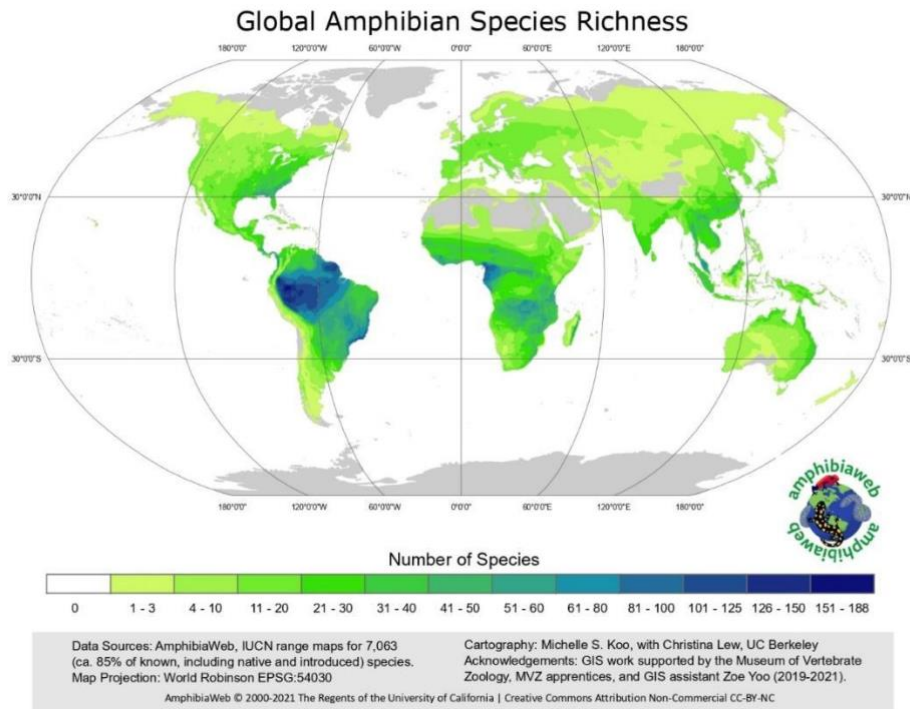
Figure 4. Global species richness of amphibians. Note the high alpha diversity in the lowland Amazonian rainforest. Source: AmphibiaWeb (2020).
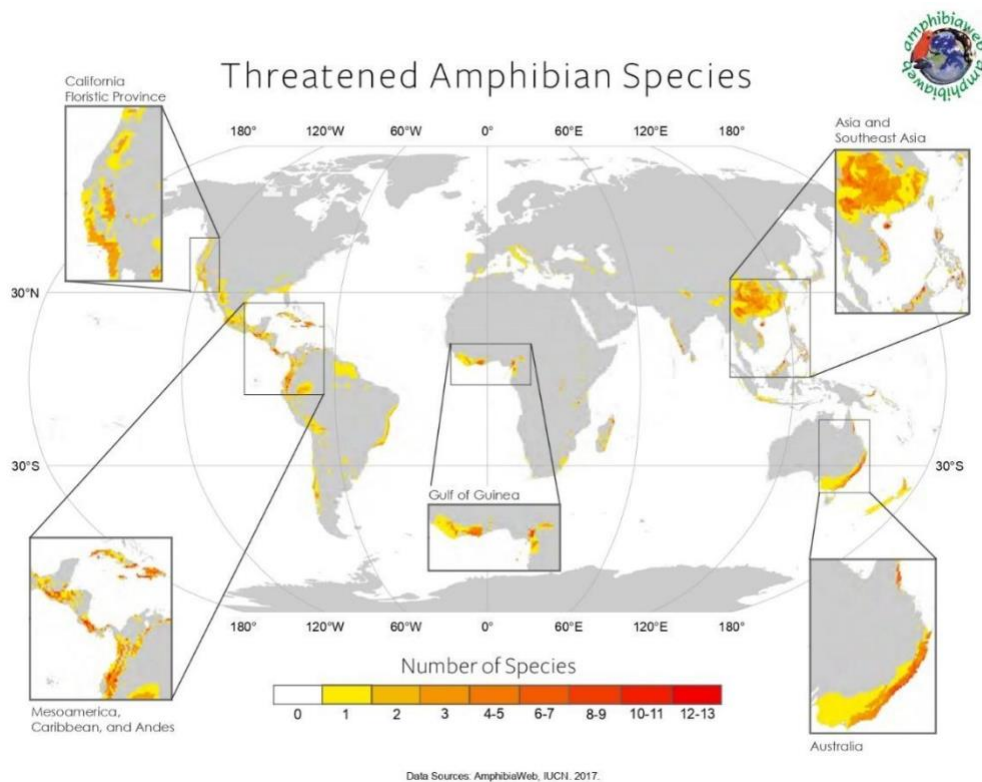

Figure 5. Threatened species of amphibians globally. Note that numerous species from the highlands of the Amazon basin are endangered. Source: AmphibiaWeb (2020).

The diversity of Amazonian amphibians remains under-described. In addition to a sampling gap that 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% (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 distributed Amazonian amphibians frequently reveal rampant cryptic diversity, uncovering many species of smaller ranges within what was once assumed to be a single, widely distributed specie (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 joint 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 diversein the Andean cloud forests (Frost 2020, 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 Amazonia, as supported by the 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 colonized repeatedly 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). Yet given their extreme vulnerability to habitat destruction, climate change, and infectious diseases, amphibian species are often considered at higher risk of extinction relative to other groups of organisms (Scheele *et al.* 2019, Stuart *et al.* 2004, Wake and Vredenburg 2008).

2.6. Diversity of reptiles

Reptiles are among the most diversified vertebrate groups in the entire planet. Currently, 11,341 species have been recorded, in 92 families and 1206 genera (Uetz and Hosec 2020). However, even with several studies related to the diversity of reptiles 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 in the region (*e.g.,* De Oliveira *et al.* 2016). The Amazon rainforest has a high diversity of reptile species, approximately 371, 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 northwest of the Amazon, indicate a greater diversity of species in relation to locations in the southeast of the 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 to 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).

Although most species of reptiles are considered terrestrial, a considerable number of species use the aquatic environment to live and perform their ecological functions. At least 40 different species strictly use the aquatic environment, and entirely depend on it for their survival (Uetz and Hosec 2020). Among them, two species of lizards (*Crocodiurus amazonicus* and *Dracaena guianensis*); three species of Boidae included in the genus *Eunectes*; as well as all species of the tribe *Hydropsini*, which includes the genera *Helicops*, *Hydrops*, and *Pseudoeryx plicatilis*; and species of coral snake, *Micrurus surinamensis*. In addition to these species, another four species of crocodilians and 16 species of turtles depend heavily on the aquatic environment to survive (Ferrera *et al.* 2017, Uetz and Hosec 2020).

2.7. Diversity of birds

Amazonia hosts the highest number of bird species in the world. With at least 1300 species, of which about 265 are endemic, the Amazon harbors approximately 38% of the Neotropic's bird species, ~4000 species (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 that represent new cryptic species (Milá *et al.* 2012). Bird diversity increases in proximity of the Andes. Topography and ecology change at an elevation of approximately 500 m, where many lowland bird species (~800) reach their upper elevational range, and many Andean reach their lowest elevational range (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 Amazonian 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 in Amazonia (*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 Amazon, 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 to the dryer eastern Amazon (Silva *et al.* 2019). However, knowledge of the evolution of Amazonian birds is a complex process and data available is still fragmentary. More sampling effort is needed to understand regional patterns of bird species richness, and community composition in the Amazon (Oliveira *et al.* 2017).

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, ~1260 species (Bonvicino and Weksler, 2012). In addition, several localities in Amazonia have the highest alpha-diversity of non-volant mammals anywhere on Earth (Peres, 1999; da Silva *et al.*, 2015). However, the number of mammal species at any single locality in Amazonia varies greatly 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%) 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% percent of all endemic species (Voss and Emmons, 1996; Paglia *et al.* 2012).

In spite of these figures, the mammalian fauna of this vast region is still undersampled, and there are not enough exhaustive surveys of mammals for the region. 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 to other groups. However, in recent years several new species have been described and new records have extended the geographic range 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 very 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 and that great dynamic 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 flows (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, about 2.5 million years ago, the ocean level rose about 150 meters and generated another transgression of the sea in the Amazon, promoting the entry of another dolphin of the genus *Sotalia*. This species adapted to freshwater conditions and gave birth to *Sotalia fluviatilis*, about 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.

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BOX 2. TRENDS IN THE DISCOVERY OF NEW SPECIES OF VERTEBRATES IN THE AMAZON BASIN

Each year new species of vertebrates are described from the Amazon, a process of discovery that started several centuries ago. The first species of Amazonian vertebrates were described by Linnaeus in 1758: 13 species of fish, 10 amphibians, 50 reptiles, 131 birds, and 51 mammals. For the analyses of tendencies in the descriptions of Amazonian species, 2406 species of fish were taken as reference (Jézéquel et al. 2020), 997 species of amphibians (GBIF: 10.15468/dl.9mgq7k), 804 of reptiles (GBIF: 10.15468/dl.uy6mw9), 2736 of birds (GBIF: 10.15468/dl.3zkc3v), and 974 of mammals (GBIF: 10.15468/dl.ttgkq4), for a total of 7827 species. 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.
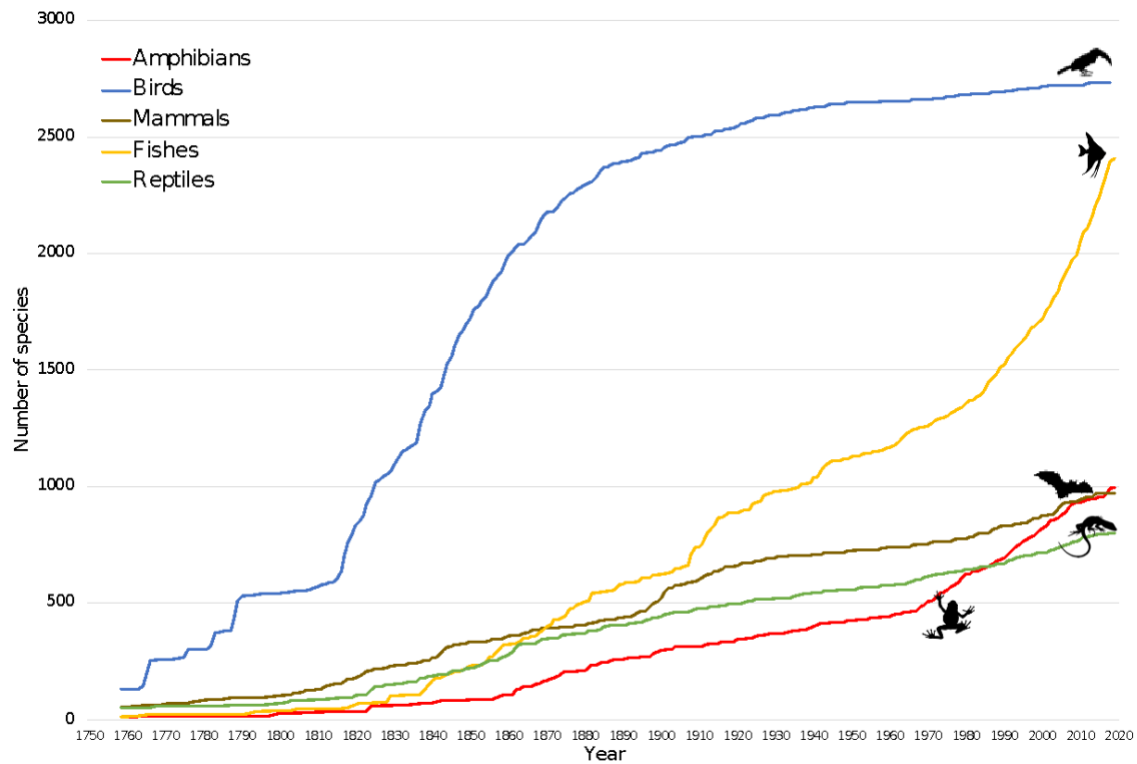
Figure B1. Species accumulation curves for five vertebrate groups from the Amazon basin.

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 about 600 species to just over 1000. Between 1940 and 1980 there was a constant increase, but it is remarkable that, since then, when the number of species was at 1355 species, there has been a sustained exponential increase in the number of species described. Indeed, between 2010-2020, the largest number (n=412) and proportion (17%) of species were described of any decade (Fig. 2). Between 1980 and 2019, 44.3% of the Amazon species were described.
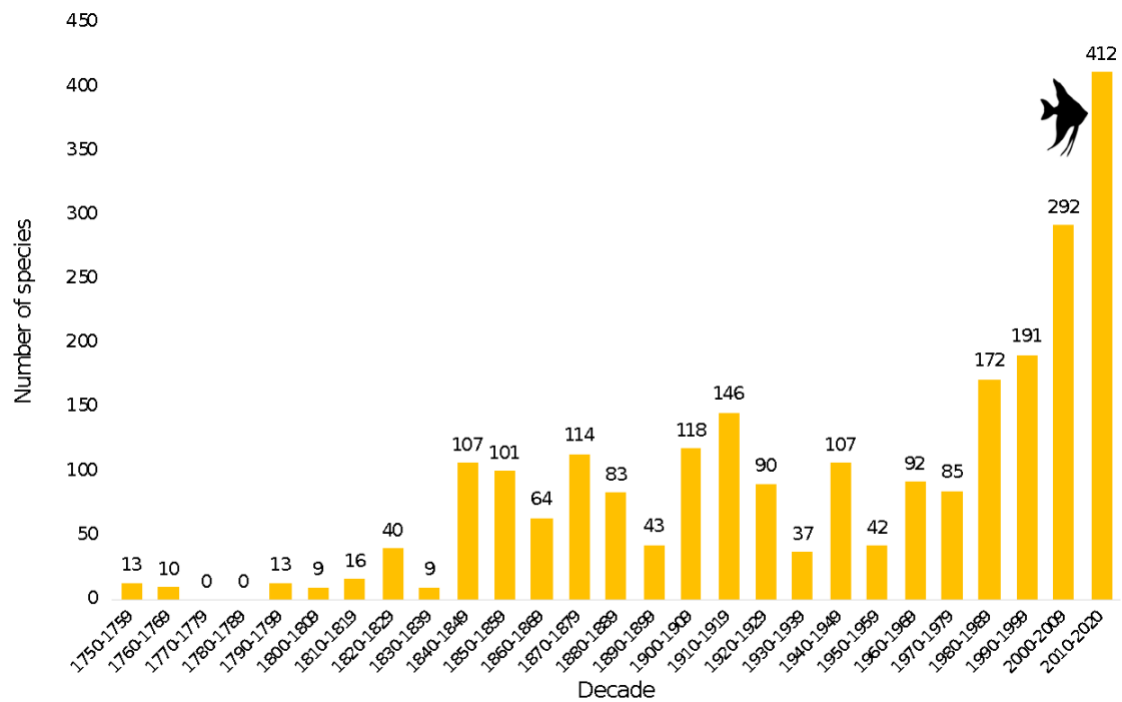
Figure B2. Number of fish species described per decade in the Amazon basin.

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 (Fig. 2). According to Jézéquel et al. (2019), The Amazon Fish database (https://amazon-fish.com/) recognizes 2406 valid fish species for the Amazon (Jéjéquel et al. 2019), with a clear tendency to continue adding new species. In time, fish may become the vertebrate group with the highest number of species in the Amazon.

Amphibians

The rate of descriptions of new amphibian species was very low until 1860, when it increased and remained relatively constant until 1970 (Fig 1). From the 1970´s onward the rate has dramatically increased, with 50.65% of Amazonian species described in the last 50 years.
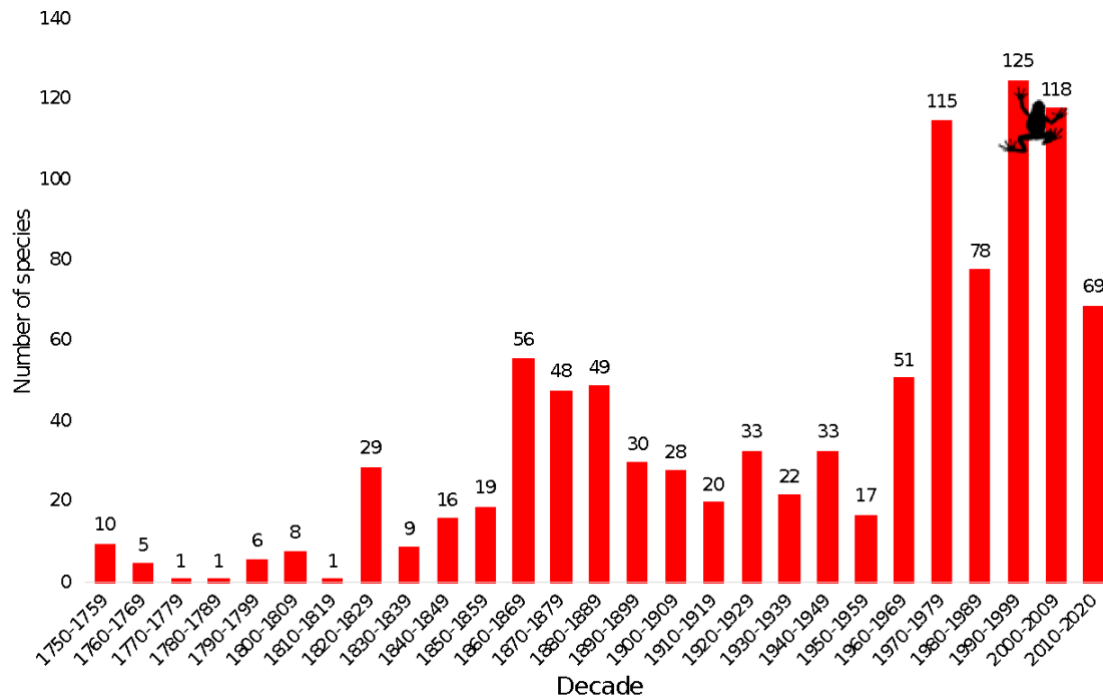
Figure B3. Number and percentage of amphibian species described by decade in the Amazon.

In the 1990s and 2000s, description peaks were reached with 125 and 118 species respectively (Fig. 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 the initial 50 species descriptions made by Linnaeus (1758), reptiles are the group of vertebrates with one of the lowest rates of descriptions (Fig. 1), and the lowest number of species described to date (804). Although descriptions have increased constantly, 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%); while 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 (Fig. 3).
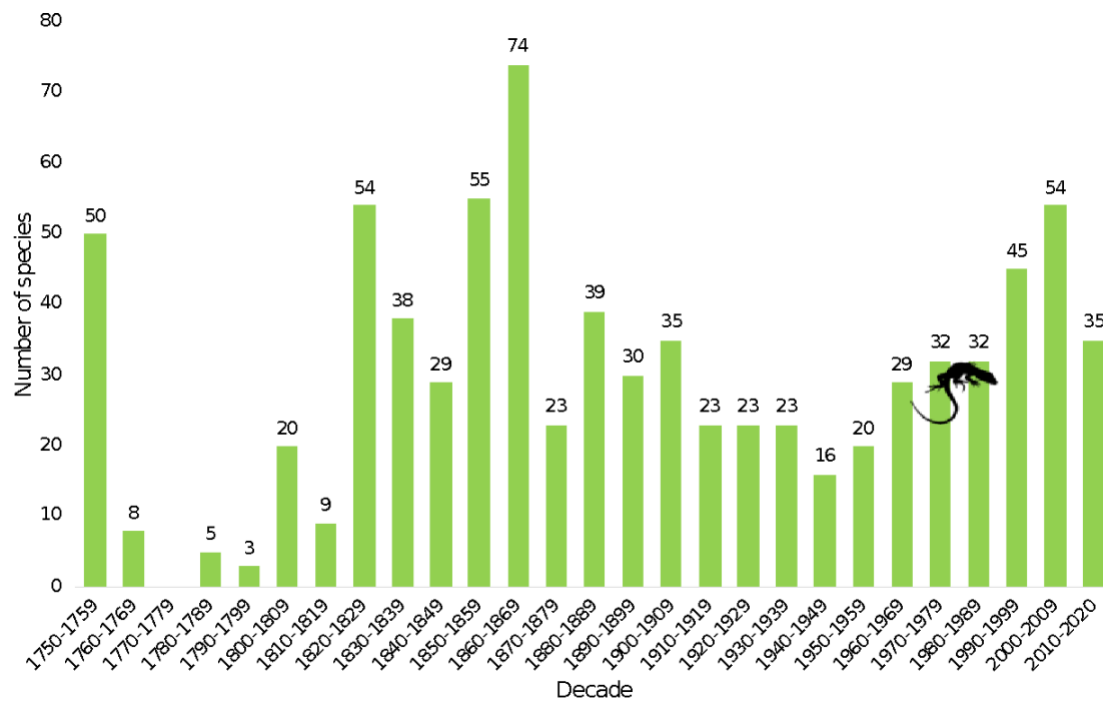
Figure B4. Number and percentage of reptile species described by decade in the Amazon.

Birds

Since the Linnaeus bird descriptions for the Amazon (150 species), it is the vertebrate group with the largest number of species, currently with 2736 species according to GBIF data (Fig. 1). Although between 1790 and 1810 there was very little increase, subsequently the number of species increased rapidly to 2500 by 1910. The peak of Amazon species descriptions occurred between 1840-1849 with 349 species added (17%), with 58.2% of Amazonian species added between 1810 and 1870. Since 1910 species descriptions have slowed down significantly, 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.

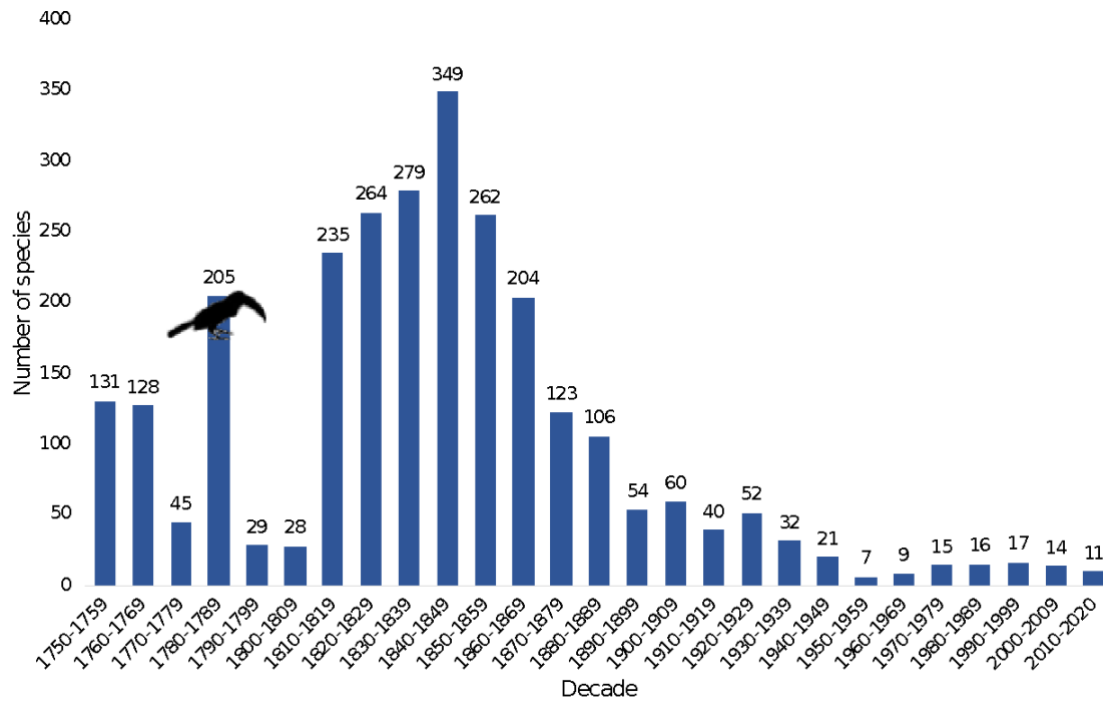**Figure B5.** Number and percentage of bird species described by decade in the Amazon.

Mammals

When descriptions of Amazonian mammal species began (51 species described by Linnaeus in 1758), they occupied second place, after birds (Fig. 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) (Figs. 1 and 6).
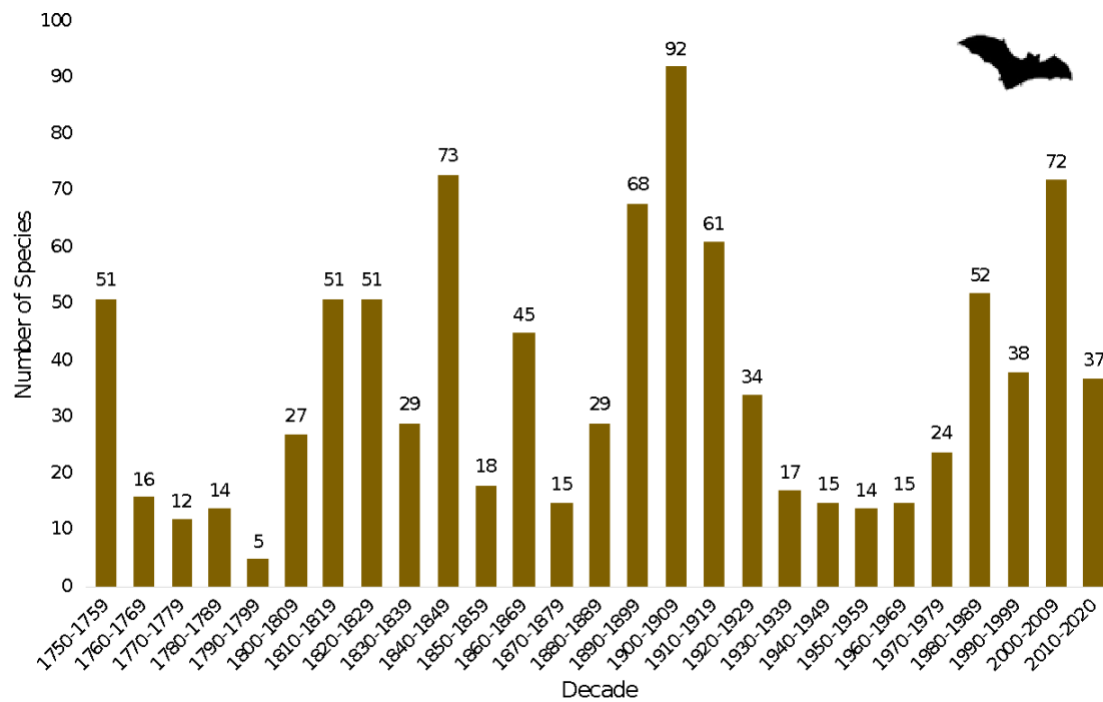
Figure B6. Number and percentage of mammal species described by decade in the Amazon.

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%, Fig. 6). The greatest potential for further new mammal species in the Amazon are in the bats, rodents and marsupials.

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 it 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. 2019) was used, while for the rest of the groups the species lists extracted from the GBIF were used, using a drawn 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.

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

If the biodiversity of plants and animals in the Amazon are still poorly known, much less can be said about the biodiversity of pathogens and parasites. Even accounting for one-third to over half of the species on Earth (Poulin 2014), these organisms are usually ignored from 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, which 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 430 wild mammal species that occur in the Amazonian region, 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 and studies investigating the community composition of parasites or co-infections are rare (Conga et al. 2014). These numbers highlight the enormous gap in the knowledge about the biodiversity of parasites in the Amazon. Protozoans are the parasite group with the largest number of studies (84 publications), but are not the group with the highest richness of species. Parasite group with the highest number of species reported interacting with wild mammals are helminths (77 species), arthropod ectoparasites (65 species), virus (62 types), followed by protozoan (29 species), bacteria (12 species), and fungi (seven species). 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* (causative agent of Chagas disease in humans), *Plasmodium brasilianum*, *Trypanosoma cruzi marinkellei*, *Trypanosoma rangeli*, the virus *Rabies lyssavirus* (causative agent of rabies in humans, and the ectoparasite *Amblyomma cajennense* (Table 2).

Table 2. Most studied parasite and pathogen species in the Amazon.

Parasite group	Most studied species	References
Virus	*Rabies lyssavirus, Laguna negra orthohantavirus, Simian foamy virus*	Deem and Emmons 2005, da Rosa et al. 1998, 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 et al. (2002), 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 Lourenco-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, da Silva et al. 2018, 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. 1981, Naiff et al. 1985, Naiff et al. 1996, Hugot et al. 2003

Concerning the arthropod-borne viruses (arboviruses), 27 different species have already been recorded infecting wild mammals in the Amazon region. From those, 16 species are known to be zoonotic, including the virus: 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 the 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 coupled with increasing social vulnerabilities are major concerns. This, added to the gap of knowledge about the biodiversity of host-parasite interactions in this region elucidates the need of understanding and building resilience into emerging diseases as a top societal challenge and research priority.

3. OUTSTANDING ECOLOGICAL PROCESSES AND ADAPTATIONS IN TERRESTRIAL AND AQUATIC ECOSYSTEMS

3.1. Plant-animal interactions

Plant-animal interactions are a central ecological process in Amazonian forests, without which these forests would cease to exist. Of the trees in the Amazonian Forest ecosystem, 80-90% rely obligately on animals for seed dispersal (Gentry 1982; Hawes *et al.* 2020), and as many as 98% of plant species rely obligately on animals for pollination (Bawa 1990). Animal dispersers are attracted to move 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 that comprises the forest. 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 Amazonia 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, complex, and include a wide variety of invertebrates and vertebrates and form the basis of the reproduction in and 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 provisioning services for humanity (Coley and Barone 1996; Fabricant and Farnsworth 2001; Food and Agriculture Organization of the United Nations *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 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 that have 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 direct effects of hunting and indirect effects of anthropogenic disturbances and particularly affects large-bodied vertebrates (Bodmer *et al.* 1997). Defaunation affects all plant-animal interactions, especially disperser and seed predation networks, with large consequences to Amazonian tree diversity (Kurten 2013; Peres *et al.* 2016), and 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 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 resilience of forest biodiversity to anthropogenic changes, and for the recovery and restoration of Amazonian systems.

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 that 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, Purus, and low biomass but high species richness in rivers of black and clear waters. In the latter, the fish depend more on non-native food (fruits, seeds, insects) or on trophic subsidies provided by migratory fishes (see below in the "Migrations fishes" section). Given the transparent conditions in clear or black waters, fish usually develop intense colors with an important function in 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 specially from the Prochilodontidae and Curimatidae families. Species such as the pirarucu (paiche, *Arapaima gigas*), which are apparently sedentary, during the low water season build nests at the bottom of the lakes and reproduce. When the water level rises, they make small lateral migrations towards the flooded forest, where the males exercise parental care of their young (Castello 2007).

In response to some of these fish migrations, large aquatic carnivores such as the Amazon river dolphin (*Inia geoffrensis*) also move after them 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 the 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 and that allows them to move their heads, which together with a long snout, allows them to catch from benthic to 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 located mainly 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, since there are frequent rises in water level that can affect nests in low parts. Another species that has developed adaptations to flood pulses in the Amazon are jaguars (*Panthera onca*), which were thought to move during these periods looking for non-flooded areas. Recent studies show that in areas like Mamirauá in Brazil, they can spend up to three months living in the treetops, feeding especially on sloths, alligators and even giant otters (Ramalho 2012; Alvarenga *et al.* 2018).

3.3. Migrations (fishes)

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, as engineering species or seed dispersal agents. Modifications or disruption of their migratory patterns by overharvesting, impoundments or habitat degradation is therefore 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 longest migrations known in freshwaters. 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 and its nursery in the estuary area 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 salmons. 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, these

goliath catfishes 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 depletion of their populations can entail profound modifications of ecosystem functions 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) in 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 whitewater rivers into clear or black waters 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 waters whereas they 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 of their nursery area downstream of the Béni River to the 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 upon the fruit falling 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 ~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). As 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).

3.4. Environmental variation and adaptation of organisms

Of the 7 million square km that the Amazon has, 800 000 square km correspond to aquatic ecosystems. The interaction between the land and the aquatic part corresponds 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 processes in the Amazon, since it generates variations of up to 15 meters 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. A good part of the vegetation is adapted to being submerged for several months and to 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 that serves as a refuge for fish and other organisms and provides food for other species such as manatees and capybaras increases (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 in the flooded forest, tributaries and lagoons in search of food, but when the water level begins to decrease, the gray dolphins (*Sotalia fluviatilis*) move to the main rivers and later Amazonian dolphins (*Inia geoffrensis*) do it to avoid being trapped in bodies of water with little food. In shallow waters, it is the time of greatest availability of food in the main rivers. With the contraction of the entire system, the fish are reduced in little space and the dolphins take advantage of it to feed. This increase in energy allows its reproduction to be synchronized with this climatic season, and the greatest amount of copulations is generated. The young are born 13 months later, also in periods of low water. 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 their body fat reserves.

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) and genetic diversity of terrestrial mammals and amphibians is 27% higher in the tropics than in the non-tropics, and the most human-affected habitats have less genetic diversity than more natural regions (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) and molecular sampling at the intraspecific level (subspecies and populations) has advanced significantly 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 of the Amazon and taxonomic groups, 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 ca. 4.6 times the second most important (Antonelli *et al.* 2018b; **Figure 6**).

Figure 6. (Figure to be included after copyright permission obtained) Amazonia 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 among regions. Dispersal events out of Amazonia 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; WIN, 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.

As it is known, both western and central Amazonia 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). Whereas, 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 western Amazonia. Finally, seasonally dry tropical forest and forests on white sands have low phylogenetic diversity (Fine *et al.* 2010; Honorio Coronado *et al.* 2015).

In the face of environmental changes and impacts, populations with reduced genetic diversity may be less capable of responding (Whitman and Agrawal 2009) and thus be 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 as in the tropics (Lande 2014). A classic example regarding the constant changes in oxygen content in Amazonian waters have resulted in 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 the high rates of alteration and turnover in the region (Quesada *et al.* 2012; Marimon *et al.* 2013; Baker *et al.* 2014).

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 where 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 responds 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 Amazon 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.

Amazonia 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 Amazonia 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 reduced 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 catfishes 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 mixed forest-savanna landscapes of the Rupununi region of Guyana, mammal species richness appears to be a major correlate of carbon cycling (Sobral et al. 2017). Interestingly, concentrations of soil carbon and carbon storage in soil and trees are greatest at sites with the highest mammal species richness. Thus, the number of feeding interactions influences the amount of carbon 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, consumer body stoichiometry, and trophic position. Fish can modulate nutrient cycling in tropical streams (Taylor et al. 2006; Capps et al. 2013), and their 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 perturbations 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 Amazon 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).

6. INCOMPLETE KNOWLEDGE OF BIODIVERSITY

While 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 the species locality data in global databases (**Figure 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, at least no data that are digitally accessible.

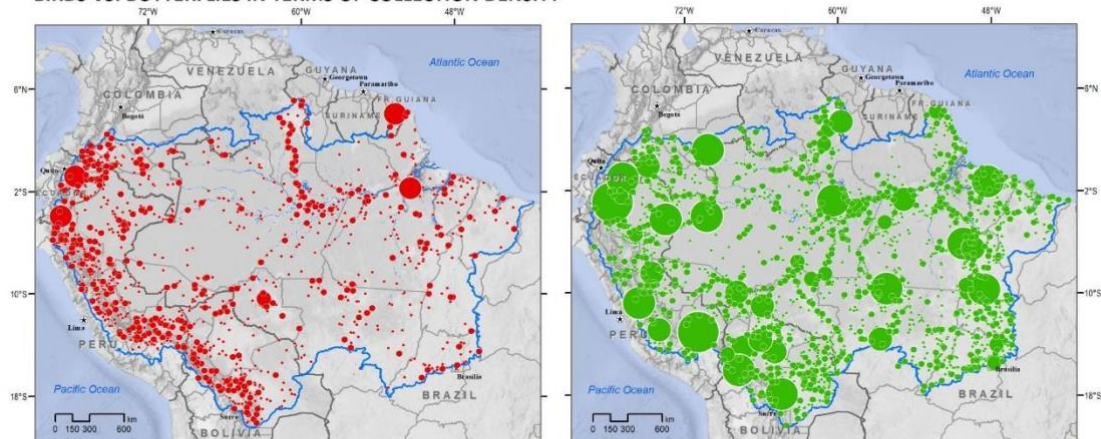BIRDS VS. BUTTERFLIES IN TERMS OF COLLECTION DENSITY

Figure 7. Butterflies (120,313 records) vs Birds (3,168,359 records) in terms of collection density. Source: GBIF, 2021. Data clustering method: Natural Jenks, Aggregation distance: 20 km.

Looking across taxa, there are also strong biases. Most of the data available are for plants or birds (>80% in GBIF). Groups like 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. Rather, 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 the ones we already know. The yet to be discovered species are certainly rarer and more restricted in their distributions than already known species. In general, it is the common and wide-spread 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.

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 the lowland rainforests, and others in Andean environments. We are still learning about the fascinating diversity of Amazonian flora and fauna, 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 resilience of forest biodiversity to anthropogenic changes, 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 fishes 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. Modifications or disruption of their migratory patterns by overharvesting, impoundments, or habitat degradation alter ecosystem processes by modifying 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 in Amazon terrestrial and aquatic biota determine species competitive ability and coexistence, species 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. Thus, scientists forecasting climate change impacts on Amazon 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. While 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.

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.

- 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 warming.

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

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10. CORE GLOSSARY

Biodiversity. The variety and variability of life on Earth, often measured at the genetic, species, and ecosystem levels.

Species richness. The number of species in a site, sample, habitat or region.

Endemism. A species with a highly localized or restrictive geographic distribution.

IUCN Red List categories. Assessment system for classifying the status of plants, animals, and other organisms threatened with extinction. There are five categories for different levels of endangerment: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR).

Terra firme. An area of rainforest off the floodplain, not subject to flooding.

Varzea. Riverine forest flooded with white water.

Igapó. Riverine forest flooded with black water.

Flood pulse. The periodic inundation and drought of a floodplain is the principal driving force responsible for the existence, productivity, and interactions of the major biota in a river—floodplain system.

Resilience. The ability of a system to continue functioning after being subjected to damage caused by disturbance.

Species traits. Species traits are defined as intrinsic characteristics of all organisms of a species, like body mass, length or height.

Functional redundancy. A characteristic of species within an ecosystem where certain species contribute in equivalent ways to an ecosystem function such that one species may substitute for another.

Migration. Back and forth movement of individuals from their reproductive grounds.

Food web. Interlocking pattern form by a series of interconnecting food chains.

Food chain. Movement of energy and nutrients from one feeding group of organisms to another in a series that begins with plants and ends with carnivores, detrital feeders, and decomposers.

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

Overharvest. The consumptive use of a natural resource beyond its capacity to replenish what has been taken.

Top predator. Predator species that are at the top of the food chain, and have no natural predators in their environment.

Trophic cascade. Indirect species interactions that originate with predators and spread downward through food webs.

Whitewater river. Rivers of the Amazon basin with headwaters in the Andes that transport large quantities of sediments. Whitewater rivers have a higher nutrient content than the blackwater and clearwater rivers.

Blackwater river. Rivers of the Amazon basin associated with areas with extremely sandy soils. Black water is essentially tea that is brewed in areas where plant compounds are not completely decomposed.

Clearwater river. Rivers and streams of the Amazon Basin that have minimal suspended sediment loads. The chemistry of lowland clearwater streams is often very similar to that of rain water.

Primary production. Assimilation (gross primary production) or accumulation (net primary production) of energy and nutrients by green plants and other autotrophs.

Natal homing. Behavioral pattern in which animals leave their geographic area of origin when young, migrate considerable distances, and then return to the area of origin to reproduce.

Phylogenetic diversity. The evolutionary relatedness of the species present in the area.

Niche conservatism. The degree to which plants and animals retain their niches and related ecological traits through space and time.

Functional diversity. The component of biodiversity that generally concerns the range of things that organisms of the same and different species do in communities and ecosystems.

Functional traits. Morphological, biochemical, physiological, structural, phenological, or behavioral characteristics that are expressed in phenotypes of individual organisms and are considered relevant to the response of such organisms to the environment and/or their effects on ecosystem properties.

Endangered species. Species threatened with extinction by anthropogenic or natural changes in their environment.

Centers of endemism. Areas rich in endemic species.

Plant-animal interactions. Critical components of many ecological processes in forests, such as herbivory, seed dispersal, and pollination.

Seed dispersal. Mechanism by which plant seeds are transported to new sites for germination and the establishment of new individuals.

Pollination. The transfer of pollen grains to a receptive stigma, usually by wind or flower-visiting animals.

Mutualism. Relationship between two species in which both benefit.

Mutualistic network. Ecological network in which one class of nodes represents one type of species (*e.g.* plants) and the other class represents another type of species (*e.g.* pollinators), while links connecting nodes of the two different classes represent the mutualistic interaction (*e.g.* pollination).

Trophic interactions. Species interactions depicting which species feed on others.

Defaunation. The extirpation of wildlife from a particular area.

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