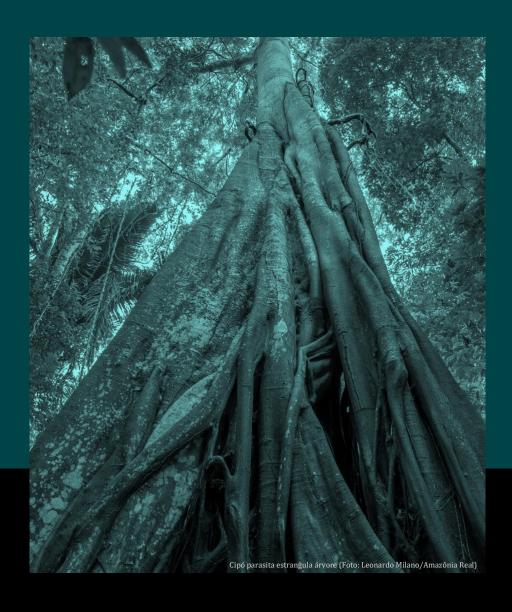
Chapter 4 In Brief

Amazonian ecosystems and their ecological functions



Amazonian ecosystems and their ecological functions

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Key Messages & Recommendations

- 1) Amazonian ecosystems exhibit high heterogeneity, with terrestrial and aquatic landscapes interacting from the slopes of the Andes mountains to the lowlands of the Amazon River basin. These interactions (including fresh and marine waters) are of critical importance to regional dynamics, contributing to the movement of animals, plants, and nutrients between floodplains and adjacent terra firme forests.
- 2) The Amazon forest is likely the richest forest area on the planet, holding an estimated 16,000 tree and 50,000 plant species, many of which are still unknown. With approximately 392 billion trees, the Amazon is home to 13% of all trees worldwide. This huge diversity is not evenly distributed, and is driven by soil geology and climate gradients.
- 3) The Amazon forest stores massive amounts of carbon (C). Spatial variation in carbon stocks is driven more by soil conditions than by climate. Amazonian wetlands store large amounts of carbon due to extensive accumulation of below-

- ground peat deposits and play a key role in maintaining the natural balance of the carbon cycle, modulating global climate change.
- 4) In order to maintain this important diversity of terrestrial and aquatic ecosystems and biological communities, it is imperative to stop deforestation and continued fragmentation.

Abstract This chapter describes the diversity of plants and ecosystems in the lowland Amazon and discusses how complex regional gradients in climate and soil conditions drive regional variability in species composition, vegetation dynamics, carbon stocks, and productivity. The Amazon River network and its role in connecting aquatic and terrestrial ecosystems through organisms and nutrient exchanges is also emphasized.

An introduction to Amazonian ecosystems The Amazon region includes the largest area of continuous tropical moist forests in the world¹, and around 10% of all known species of animals and plants are estimated to live there. Covered mostly by nonflooded *terra firme* forests, it also contains the largest tropical floodplain system². Based on geomorphology, species composition, and structure, forests can

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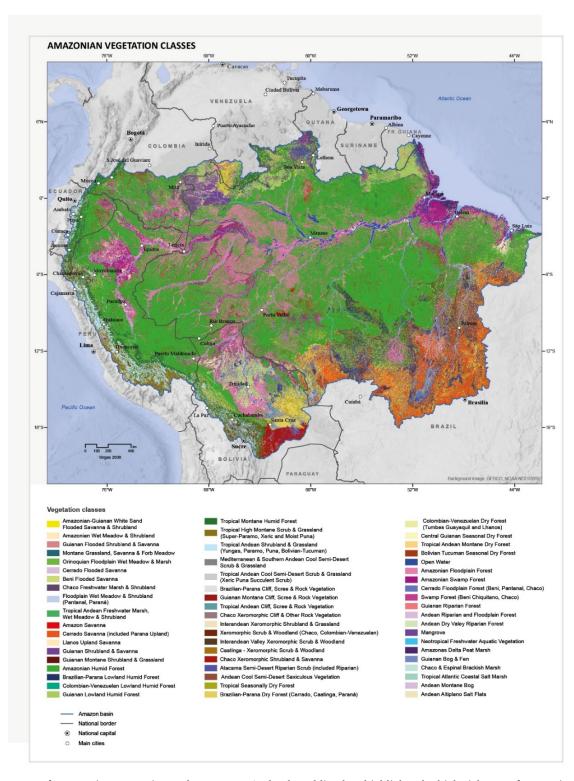


Figure 4.1 Map of Amazonian vegetation and ecosystems⁴. The dotted line box highlights the high richness of vegetation and ecosystems found along latitudinal and altitudinal gradients. Sources: ^{5,6}.

be classified into *terra firme forests*, seasonally flooded forests (*várzea, igapó*), swamp forests, and white sand forests (*campinarana*)³. Freshwater ecosystems cover more than 1 million km² and consist of three main water types – white, black, and clear waters – which differ in their origin and sediment composition.

From the high Andes to the Atlantic Ocean Ecosystems and changes in the structure and composition of vegetation can be depicted along an elevation gradient. At the highest elevation, the tree-less Andean páramo is adapted to cold temperatures and extreme solar radiation and borders above 3,000 m. At the lowest elevations are the tree-dominated Amazon lowlands (<500 m) (Figure 4.1)^{4,5} 6. Montane forests (2,500 – 3,900 m) are among the richest ecosystems found in the tropical high Andes⁷, identified as the world's most threatened hotspot for biodiversity owing to deforestation and land use changes8. Andean premontane forests include mixtures of species found in lowlands or upper montane forests, and a set of endemic species that are altitudinal specialists9.

Lowland Amazonian terrestrial ecosystems The composition of Amazonian forests appears to be determined by soil fertility and annual rainfall. Cardoso et al. (2017)¹⁰ recorded 14,003 species, 1,788 genera, and 188 families of seed plants in Amazonian lowland rainforests. More than half of the species diversity of seed plants in Amazonian rainforests comprises shrubs, small trees, lianas, vines, and herbs. Three of these top 10 families are exclusively herbaceous (Araceae, Orchidaceae, and Poaceae^{11,12}). It is estimated that the Amazon may hold close to 16,000 tree species, 10,000 of which have been collected in the area^{13,14}.

Ten families contribute to 65% of all Amazonian trees, including Fabaceae (beans) and Arecaceae (palms). Interestingly, palms are the second most abundant family in the Amazon and contribute seven of the most abundant species, but do so with few species as compared to the most abundant and species rich family, Fabaceae.

Species diversity is not evenly distributed across the Amazon (Figure 4.2)^{5, 6,15,16,17}. The highest diversity is found in the northwestern and central Amazon, where one hectare may contain over 300 tree species^{18,19}. Species richness is highest in dryland (*terra firme*) forests, especially those of the more fertile western Amazon, and lowest in flooded, swamp, and white sand forests.

White sand forests (also known as *campinarana*, Amazonian caatinga, or Varillal) are found on pockets of highly leached deposits of white-sand³ and occupy roughly 3-4% of the Amazon. They are generally species poor and, because of their isolation in small patches, may never recover species that have been lost²⁰.

Savannas and grasslands These occupy 14% of the basin (including the Tocantins-Araguaia basin), including some *terra firme* areas of the southeast of the Brazilian Amazon, and some permanently or seasonally flooded sites, as in Beni in Bolivia. Patches of open savanna can also be found in areas of leached white sand, or on degraded lands subject to fire.

Fresh water and wetlands

Rivers, lakes, and forest streams Fresh water ecosystems in the lowland basin include rivers, lakes, and streams, in addition to areas with permanent, temporary, or seasonal standing or flowing water, or with saturated soils, such as swamps. These ecosystems are a fundamental part of the large fluvial system of the Amazon, occupying 800,000 km², or 14% of the basin²¹. The Amazon basin consists of the main river itself and approximately 270 sub-basin tributaries (Figure 4.3). These rivers are generally classified as white water, clear water, and black water, based on the color of the water, which is related to transparency, acidity (pH), and electrical conductivity²².²³.

White-water rivers (such as the Amazon's main stem, and the Juruá, Japurá, Purus, Marañón, Ucayali, and Madeira Rivers) originate in the Andes⁶. White-water rivers have near-neutral pH and relatively high concentrations of dissolved solids, which makes them conductive^{23,24}; they are surrounded by *várzea* floodplain forests and extensive floating meadow wetlands²⁵. Clear-water rivers have their upper catchments in the Cerrado region of central Brazil and eastern Bolivia, draining the ancient Brazilian shield. The pH of clear-water rivers varies from acidic to neutral, depending on the soil²². Black-water rivers have their origin in the lowlands; they are translucent, high in dissolved organic carbon, and low in nutrients.

Amazonian lakes are the result of fluvial processes in depressions or flooded valleys. Few areas within the lowland Amazon are more than 100 m above the river surface, resulting in a dense network of small streams and lakes. Stream fauna depend on energy inputs from the surrounding forest (e.g., insects and plant material), and much of the terrestrial flora and

fauna in turn depend on streams. This intricate connection continues as the streams coalesce downstream into larger rivers.

Freshwater wetlands Wetlands are ecosystems at the interface between aquatic and terrestrial environments, with biota adapted for life in water and water-saturated soils^{26,27}. Wetlands cover 2.1 million km² and are divided into two main groups²⁶ those with relatively stable water levels (e.g. Mauritia flexuosa palm swamps) and those with oscillating water levels (e.g. floodplain forests and mangroves). Some of these wetlands are dominated by forest and broadly distributed, while others are found only in specific regions within the basin, such as the savannas of the Llanos de Moxos (Bolivia), and Bananal savannas (Brazil) which are seasonally-inundated grasslands, sedgelands, and open woodlands²⁸ (Figure 4.1).

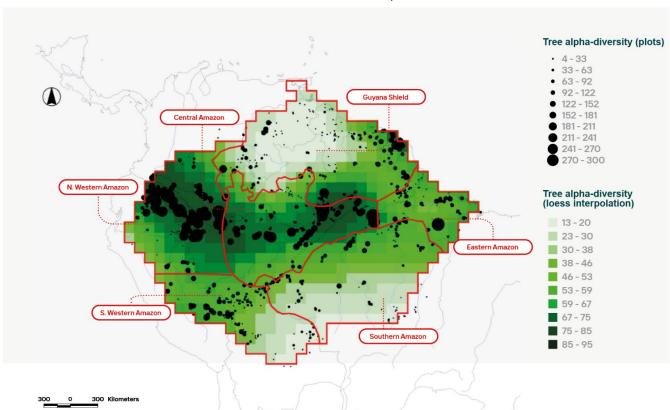


Figure 4.2 Map of the Amazon's tree α -diversity¹⁵, based on data from field plots of 1 hectare (black dots) averaged across grid cells of \sim 111 km (green gradient). In red lines, the six regions of the Amazon as used in this chapter^{11,16}.

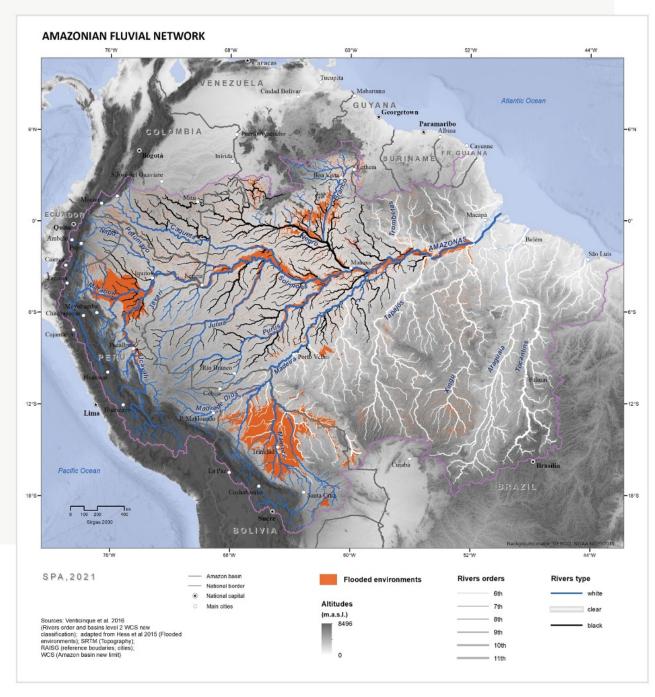


Figure 4.3 Amazon River network (from Venticinque et al. 2016⁵), indicating distribution of flooded environments (modified from Hess et al. 2015²¹).

Floodplain forest Seasonally-flooded forests cover 0.76 million km², or 11% of the basin, and are subjected to predictable, long-lasting, annual floods²⁶,

exhibiting strong interannual variability. These forests are flooded due to their low topographic location, small slopes and poorly drained soils. Flooding

may last up to six months and water levels may fluctuate up to 10 m between the dry and flood seasons²⁹.

Floodplain forests along white water rivers are known as *várzea* in Brazil and represent the most extensive type of flooded forest in South America (covering approximately 456,300 km²)³0. Amazonian floodplain forests contain around 1,000 species of trees, making them the most diverse in the world³¹-³³3. A significant number of tree species (40% of the most common central Amazonian *várzea* species), are found only in floodplain forests; only ~31% of tree species in *várzea* are also found on *terra firme*²⁵5.

Igapó forests cover around 302,000 km²; they are seasonally flooded up to 9 m deep by black (or clear) water rivers^{26,34}. Due to the lack of soil nutrients, tree abundance and biomass is much lower in *igapó* forests than in *várzea* and *terra firme*^{30,35,36}. Montero et al. (2014)³⁷ recorded 243 tree species, 136 genera, and 48 families for the *igapó* forest.

Permanently flooded swamps Permanently flooded or waterlogged areas (swamps) occupy a small area compared to other ecosystems in the Amazon (80,000 km², or 1%). Extensive palm formations are very characteristic of Amazonian swamps. They are found from the lowland plains to the Andean foot hills, up to 500 m of altitude, always associated with highly stagnant black water³⁸, such as in permanent wet depressions within the savanna landscape³⁹. There are also permanent swamp areas with rooted plants in channels or depressions within the alluvial plain^{40,41}.

Flooded savanna The seasonally-flooded savannas of the alluvial plain cover 200,000 km² ⁴⁰ and represent 6% of flooded plant communities⁴². They occur in the north (Roraima and Rupununi) and south (Beni savanna) of the Amazon, and along the Cerrado belts in Brazil and the Guianas, and have strong climatic seasonality (several dry months)²⁶. Flooding is mainly influenced by rainfall and the overflow of rivers during a 3- to 5-month period; however, in a matter of hours the flooding percolates into the soil and there is no permanent standing water, except in

low places and depressions linked to rivers. On alluvial plains of white water rivers, Poaceae species (grasses) predominate, followed by Cyperaceae (sedges)⁴³.

Mangroves Mangroves occupy relatively small areas in a narrow littoral belt along the Atlantic Ocean and in the Amazon estuary. Mangroves are flooded by salt or brackish water, are poor in number of tree species, and generally uniform in structure, not exceeding 10 m in height. The largest mangrove area measures at least 7,000 km² and extends southward from Belém⁴⁴.

Ecosystem functioning

Primary productivity, nutrients, forest dynamics, and decomposition in terrestrial ecosystems In the Amazon, climatic factors exert the greatest influence on gross production, but a wide range of other factors related to soil, disturbance, and species composition are also influential in determining how captured carbon is allocated and how long it is stored in trees and sinks. Spatial variation in Amazon biomass carbon stocks and dynamics are driven more by soil conditions than climate. Mortality rates vary greatly across the Amazon, being higher in the western and southern regions (2.2 to 2.8% per year), than in northern and eastern central regions (1.1 to 1.5% per year^{46–48}).

Climate nevertheless affects rates of woody biomass production, with consequences for sustaining productive forest ecosystems⁴⁹. However, not all Amazon forests appear to be impacted by the climate across large areas; shallow water tables in the central and western Amazon shields plants against drought¹². Higher temperatures and longer dry seasons are projected for the southern Amazon basin⁵⁰ and likely to induce changes in decomposition rates and patterns. Any changes in decomposition processes will have profound impacts on the rate and pattern of nutrient cycling, with implications for forest plant and animal community dynamics.

Primary productivity, nutrients, vegetation dynamics, and decomposition in freshwater ecosystems As in terre-

strial ecosystems, the functions of aquatic ecosystems comprise biochemical activities such as plant and algae productivity, decomposition of dead organic matter, and processes related to the flow of sediments, energy, and nutrient cycling⁵¹. Flows of energy and nutrients are prime examples of the dynamic nature of aquatic ecosystems, and the Amazon is no exception. By connecting rivers with floodplain habitats, floods provide a mechanism to compensate for limited in-situ algal productivity⁵². Recent models estimate that 38% of Amazon wetlands form peat deposits.

The aquatic-terrestrial transition zone Interactions between terrestrial and aquatic ecosystems are among the most important processes in the Amazon. Terrestrial primary production (i.e. organic matter and nutrients) is captured when floodwaters rise; this material decomposes or is consumed by organisms, becoming the basis of the aquatic food chain^{53,54}. Part of this productivity returns to the river's main stem through the many organisms that move between the floodplains and the river, including large numbers of migratory fish^{55,56}. Floodplains play crucial roles as feeding grounds and nursery areas for many fish^{57–59}.

In floodplain lakes connected to white water rivers, the lack of currents allows sediment to settle and greater water transparency. This allows phytoplankton to grow, fueling a zooplankton-based food web. Thus, floodplain lakes play a key role as nurseries and feeding grounds for juvenile fish of commercial value⁶⁰. These fish are also important seed dispersers in the Amazon^{55,61,62} (see Chapter 3).

Floods also affect the movement of terrestrial animals between floodplain and adjacent *terra firme* forests. During the flood period, abundant fruits attract frugivorous monkeys to floodplain forests, while kingfishers track fish movement to the interior of flooded forests. Moreover, flooding enhances habitat heterogeneity in floodplain forests, driving the development of unique bird, bat, and amphibian communities not found in adjacent *terra firme* forests^{63–65}.

Conclusions Between the Andean mountains and the Amazonian plain there is a diverse mosaic of ecosystems consisting of forests, savannas, and swamps. The Amazon rainforest is probably the richest forest area on our globe, containing approximately 392 billion trees. This enormous diversity is not evenly distributed throughout the basin. The Amazon River network plays a key role in connecting terrestrial and aquatic ecosystems. Seasonal floods facilitate the transport of nutrients, which is fundamental to regional dynamics. Thus, the key to understanding the ecology of the Amazon is to understand the integration between terrestrial and aquatic ecosystems.

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