Science Panel for the Amazon (SPA)

Working Group 2

BIODIVERSITY AND ECOLOGICAL FUNCTIONING IN THE AMAZON

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CHAPTER 4: AMAZONIAN ECOSYSTEMS AND THEIR ECOLOGICAL FUNCTIONS

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CHAPTER 4: AMAZONIAN ECOSYSTEMS AND THEIR ECOLOGICAL FUNCTIONS

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. KEY MESSAGES

- Between the Andean mountains and the Amazon plain there is a diverse mosaic of ecosystems and vegetation formations represented by biomes of forest, savannas and swamps; the key to understanding the ecology of the Amazon is to integrate functional processes, between terrestrial and aquatic components, across multiple biophysical gradients, from the continental divide to the ocean.
- The Amazon forest with 5.79 km^2 is likely the richest forest area on our globe, holding an estimated 16,000 tree species and perhaps over 50,000 plant species, many of which still unknown. With close to 400 billion trees, the Amazon is home to 13% of all trees world-wide.
- Species composition is not evenly distributed across the basin but is determined by soil geology and climate. The richest forests are found in Western Amazonia but for comprehensive conservation protected areas should be present across the basin. Forests in western Amazonia, on fertile grounds, are species rich, have high stem turnover and low above ground biomass, compared to forests in central and east Amazonia, that are mainly found on poor soils, have slow turn-over and higher above ground biomass.
- The Amazon river basin holds the largest tropical wetland on earth and together with the vast number of rivers is not only the biggest fresh water store but holds 15% of fish species on earth. The transfer of nutrients and energy of Andean origin is carried out by massive annual fish migrations that meet the areas of white and black waters of the river basin, contributing to the balance in regional productivity.
- Forest composition is already being affected by climate change, with the mortality of wet-affiliated genera having increased in places where the dry season has intensified most. Such changes may take a long time to reverse or may prove irreversible.

- Amazonian ecosystems result from a mixture of terrestrial and aquatic landscapes in an extensive flood plain, whose dynamics derive from the slopes of the Andes mountains to the Amazon river basin. The contact areas or ecotones between terrestrial and aquatic ecosystems (fresh and marine waters) are of critical importance for the dynamics of the whole region, contributing to the movement of animals, plant propagules and nutrients between floodplain and adjacent terra firme forests which promote habitat heterogeneity.
- Because of its size the Amazon forest is a huge store for carbon. Spatial variation in Amazon biomass carbon stocks and dynamics are driven more by soil conditions than by climate, and more by spatial variation in mortality than productivity.
- Amazonian wetlands also store large amounts of carbon due to the extensive and deep accumulation of below-ground peat deposits (e.g., > 3 Pg C in north-western Amazonia) and play a key role in maintaining the natural balance of the C cycle, modulating global warming.

ACRONYMS AND ABBREVIATIONS

asl = above sea level

ATTZ = Aquatic terrestrial transition zones

C = Carbon

C cycle = Carbon cycle

C emission = Carbon emission

CO_2 = Carbon dioxide

C stocks = Carbon stocks

CUE = Carbon Use Efficiency

GPP = Gross Primary Productivity

kT = Rate to temperature

Mg C = Tonne of carbon

NPP = Net Primary Productivity

Pg C = Petagram of carbon

pH = potential of hydrogen

Q_{10} = Temperature sensitivity

SE = Standard Error

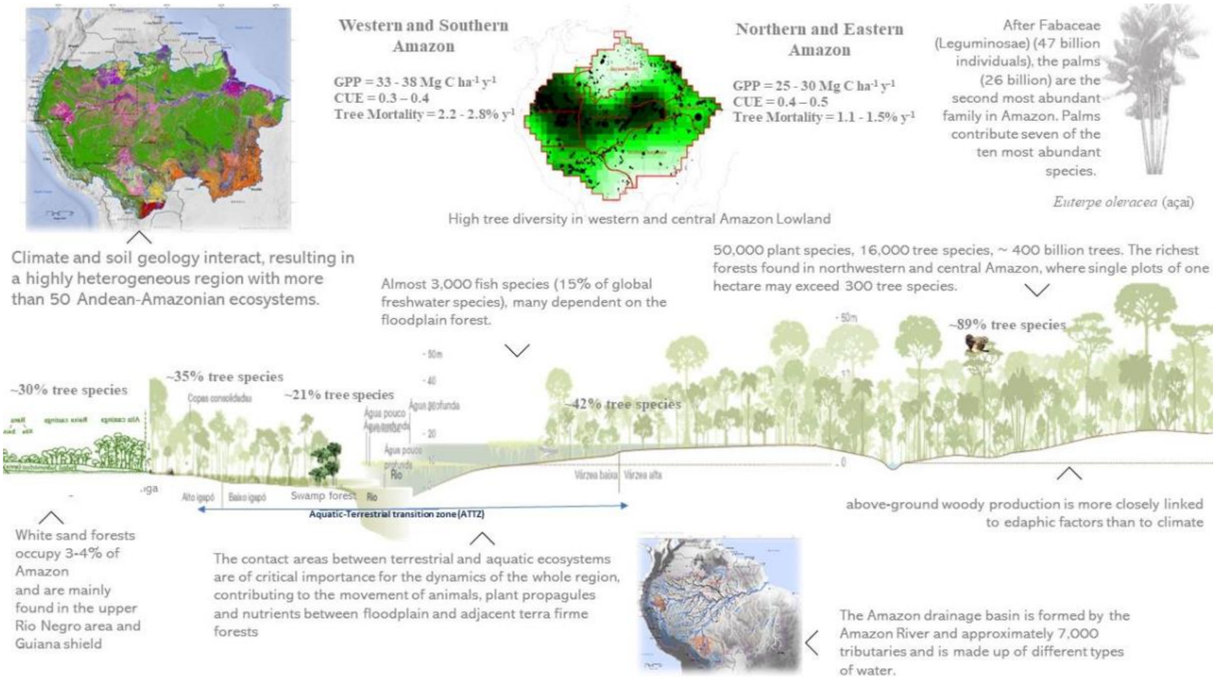
µS/cm = Microsiemens Per Centimeter

ABSTRACT

The Amazon biogeographical region covers ~7 million km^2, 5.79 km^2 of which are lowland tropical rainforest. Based on geology, the Amazon lowland forest area can be divided into six regions. The Guyana shield and Brazilian Shield (Southern Amazonia) regions are on very old, nutrient poor, soils, while the Western Amazonian regions (northern and southern) and the regions along the Amazon River are mainly built from more recent sediments with Andean origin and of variable nutrient richness. The six regions are characterized by differences in soil fertility, rainfall, causing differences in above ground biomass, productivity and tree turnover. There is still strong debate concerning the total plant species richness of Amazonia. A well supported estimate for trees (dbh > 10 cm) is 16,000 species, ~11,000 of which have been collected, while estimates of the total flora range from 15,000 – 55,000 species. As in much of the tropics, the Fabaceae (the bean family) are the most species-rich of the major woody groups in Amazonia. South America and Amazonia are also renowned for the abundance and diversity of palms. While most ecosystem vegetation models emphasise climate and carbon production processes, these are not sufficient to understand how Amazon forest ecosystems vary spatially. In particular, long-term observations with plots show that spatial variation in Amazon forest biomass and stem dynamics are driven more by soil conditions than climate, while carbon stocks are constrained as much by soil physical features and tree floristic composition as by productivity. The key effects of soils on Amazon ecosystem function extend also to animals and their important functions, including herbivory, seed dispersal, and insect activity. The key impact of soil nutrients extends to Amazon rivers too, which are classified as white water (carrying sediments from the Andes), clear water (draining the two shield areas), and black water (draining white sand areas). The nutrients associated with each major river class also influence the floodplain forest ecology and species, with *igapó* in sediment-poor clear and black waters and *várzea* (*tahuampa* in Peru) with white, sediment-rich waters. Climate impacts become stronger towards the margins, and some Amazon forests are already close to the thermal and hydrological limits of sustaining productive forest ecosystems. Already, tree mortality rates have been increasing in many intact forests, and Amazon forest composition has been affected by recent droughts, with the mortality of wet-affiliated genera increasing in places where the dry season has intensified most. Key areas of uncertainty include the extent to which recent climate change has caused a slowing of the Amazon carbon sink, and if intact forests will now lose carbon - or whether the shallow water tables and rich biodiversity of many Amazon forests will help protect against climate change.

Key words: Amazonian ecosystems, Aquatic ecosystems, Forest Dynamics, Ecological features, Ecosystem processes, Interactions, River system, Terrestrial ecosystems.

GRAPHICAL ABSTRACT [1]



1. AMAZONIAN ECOSYSTEMS: AN INTRODUCTION

The Amazonian biogeographical region covers about 8.4 million km^2 of northern South America, including the lowland Amazon and Orinoco river basins and adjacent upland areas of the Guiana and Brazilian Shields (see Chapter 2). The Amazon River basin (7.3 million km^2), including Tocantins and Araguaia basins, covers 41% of South America, encompassing two of the major South America biomes, tropical moist forests and tropical savannas (Coe et al 2008). The Amazon region is considered one of the most important ecological regions in the world, because it includes the largest area of continuous tropical moist forests estimated to cover 5.74 million km^2 (Ter Steege et al. 2015) and an estimated 10% of all known species of animals and plants on Earth are estimated to live there (Chapter 2). It also contains the largest tropical floodplain system (Keddy et al. 2009), constituted by a rich mosaic of terrestrial,

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[1] general diagram of Amazon ecosystems is credited to National Geographic

aquatic and transitional ecosystems subjected to seasonal or permanent waterlogging (Salo et al. 1986) (**Figure 4.01**).

The ability of ecosystems to capture, process and store carbon and other nutrients is determined by key climatic, edaphic, and biological factors. Amazonia, with the largest tropical rainforest on the planet, covering ~5.74 million square kilometres, spread over nine countries, encompasses significant differences in precipitation regimes but even greater differences in terms of the geological origin, age, and nutrient richness of the soils that support its ecosystems (see Chapter 1). Here we emphasise the role of these factors in controlling forest composition and processes especially those related to productivity and forest dynamics.

Based on geomorphology, species composition and forest structure, Amazonian forests can be classified into terra firme forest, seasonally flooded forests (várzea, igapó), and swamp forests. Extremely poor white sand forests may be found, especially in the upper Rio Negro area and Guianas (see Adeney et al. 2016). Freshwater ecosystems cover more than 1 million km^2 and consist of three main water types – white, black and clear waters, which differ in their origin, sediment composition, and other characteristics.

In this chapter we summarize the information on Amazonian ecosystems and their ecological functions, with a strong focus on its trees. We start with a short description of the vegetation types of the Andes, and a more detailed description of the lowland Amazonian terrestrial vegetation types and the vast wetlands, included in the area. We continue with an analysis of the main ecosystem functions (e.g. terrestrial and aquatic), with emphasis on productivity and carbon sequestration. The aim of this chapter is to show the enormous variation of vegetation types, their diversity and functioning, and how this is affected by soil, climate and flooding dynamics.

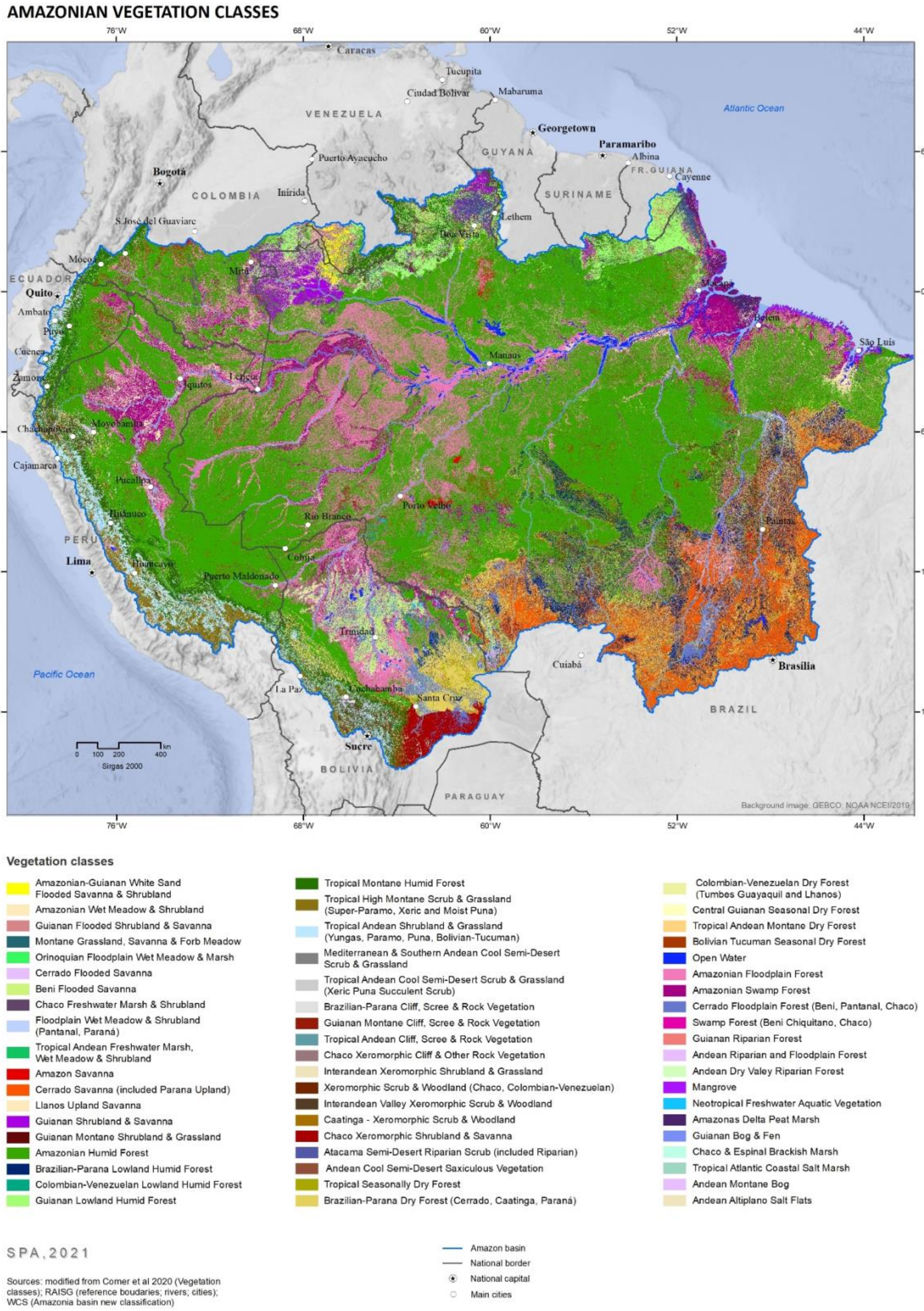


Figure 4.01 Map of Amazonian Vegetation and Ecosystems (source: Comer *et al.* 2020). The solid gray box highlights the high richness of vegetation and ecosystems found in the latitudinal and altitudinal gradients in the Amazon (see Figure 4.04 for detail).

1.2. Vegetation types from the High Andes to the Atlantic Ocean

Alexander von Humboldt's *Tableau physique* (Humboldt 1805) is, arguably, the first published overview of plant composition of northern South America as a region (**Figure 4.02**). His travels extended from the Pacific to the Atlantic Oceans and passed Chimborazo, the highest equatorial volcano in Ecuador (Ulloa Ulloa & Jørgensen 2019). Humboldt depicted the biotic and physical characteristics, and changes in vegetation structure and composition along an elevation gradient, from the tree-dominated lowlands to the treeless páramo bordering the snow line.

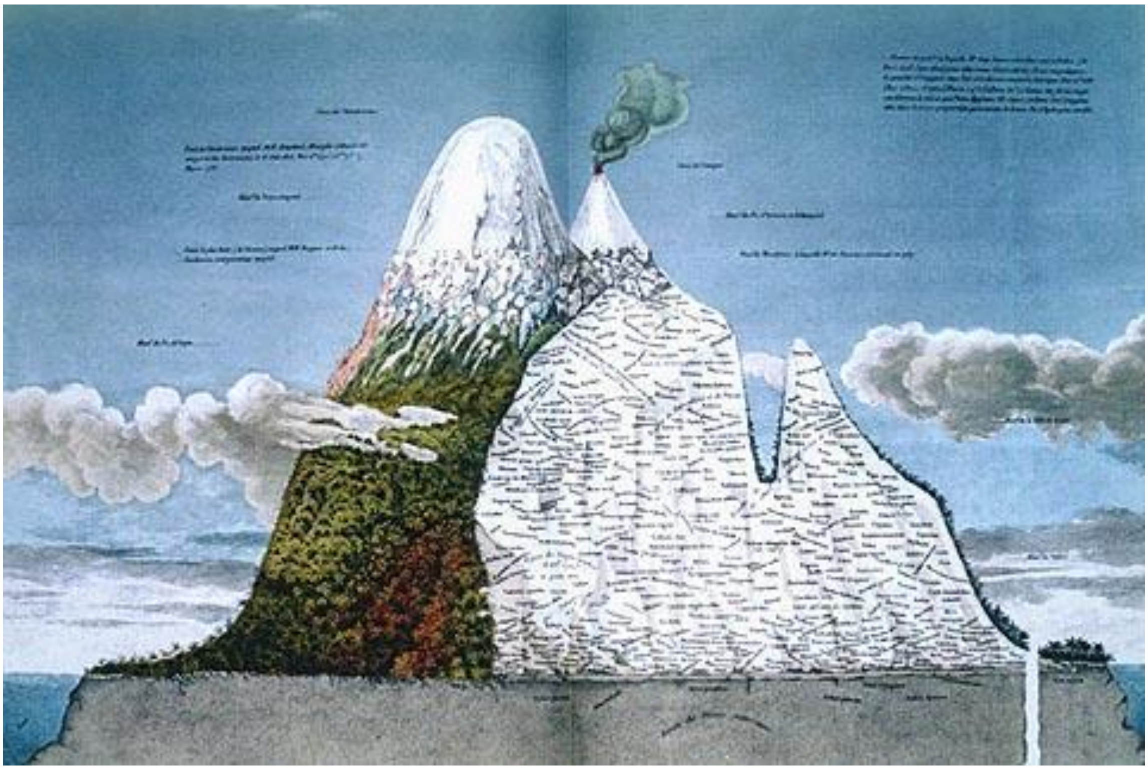


Figure 4.02. Alexander von Humboldt's *Tableau physique* (Humboldt 1805) graphic overview of plant communities, from the Pacific to the Atlantic Ocean and passing over the Andean mountains. Reproduced with permission from the Peter H. Raven Library, Missouri Botanical Garden (https://www.biodiversitylibrary.org/page/9869921).

Plant communities in the high Andes (above 3,000 m) are known as 'páramo' in the more humid areas of the northern Andes of Venezuela, Colombia, and Ecuador, and 'Jalca' in northern Peru (Madriñán et al. 2013); 'puna' is found in the southern, drier Altiplano of Peru and Bolivia (Sánchez-Vega & Dillon 2006). Páramos and punas are grass-dominated ecosystems with plants uniquely adapted to these extreme environments of cold temperatures, low pressure, and extreme solar radiation, with prominent rosette forming plants, such as those in the genera *Espeletia* and *Puya.* Only a few species of trees, such as those in the genera *Buddleja, Gynoxys*, and *Polylepis* reach highest elevations, up to 4,700 m (Hoch & Körner 2005).

Upper montane forests extend in humid sites from 2,500 to 3,900 m elevation. Montane forests are among the most species rich vegetation types to be found in the tropical high Andes (Churchill et al. 1995). These forests are 5 to 20 m tall with emergent trees reaching to 35 m or more; but with smaller individuals at the treeline and in places where soils are shallow or disturbances altered the vegetation in the past. Lower-montane forests are found at middle elevations, centered around 2,500 m and humid to very humid forests found at 1,000 m can be as diverse and complex as forests found in humid tropical lowlands. Intermontane valleys cut through the tropical Andes reaching as low as 2000 m. Andean and Amazonian species and ecosystems form spatial mosaics in the alluvial valleys above 1.000 m, surrounded by slopes covered by montane forests (Josse et al. 2009). Below 1000 m the Andean submontane forests gradually change into the Amazonian lowland forests, here below 500 m, that cover most of the basin.

2. LOWLAND AMAZONIAN ECOSYSTEMS

2.1. Terrestrial Ecosystems

2.1.1. Lowland rainforests

Amazonian lowland rainforests cover approximately 5.79 million km^2 over nine countries (ter Steege et al. 2013, ter Steege et al. 2015). Mean annual rainfall varies from especially humid forests in the northwestern Amazon (over 3000 mm) to drier, more seasonal systems in the southern Amazon (1500 mm) (Espinoza-Villar et al., 2009). Based on the maximum geological age of the soil producing materials, the area has been divided into 6 regions (Quesada et al. 2011, ter Steege et al. 2013). These six regions and their patterns of tree diversity are displayed in **Figure 4.03**.

Soils in north-western and south-western Amazonia (parts of Colombia, Ecuador, Peru, and also extending into western Brazil and parts of Bolivia), originate from recent (Holocene and Quaternary) Andean riverine sediments or Tertiary estuarine deposits. These are typically more nutrient-rich than the much older, clays of Eastern Amazonia, and soils derived from the ancient Precambrian Shields of the Guyanas and parts of Brazil (Quesada et al. 2010, 2011) but are also less physically favourable to trees, being often shallower, with poorer structure and more prone to water-logging. Overall, therefore, a rainfall gradient runs from the northwest (wet) to the south and southeast (drier), and a more complex soil gradient runs almost orthogonal to this, from the west and south-west (more fertile) to the east and northeast (less fertile). As a result, lowland forests of southwest Amazonia have very similar hot, moist and somewhat seasonal climates to the distant forests of the Guyanas, yet soils which are more fertile and in terms of physical structure and rooting depth often much less favourable - and have almost complete turnover of dominant tree species (ter Steege et al. 2006). Overlaid on these large-scale basin-wide patterns are complex regional-scale and landscape-scale geomorphological, fluvial, edaphic and hydrological variations which help create the great biological richness and diversity of Amazon ecosystems.

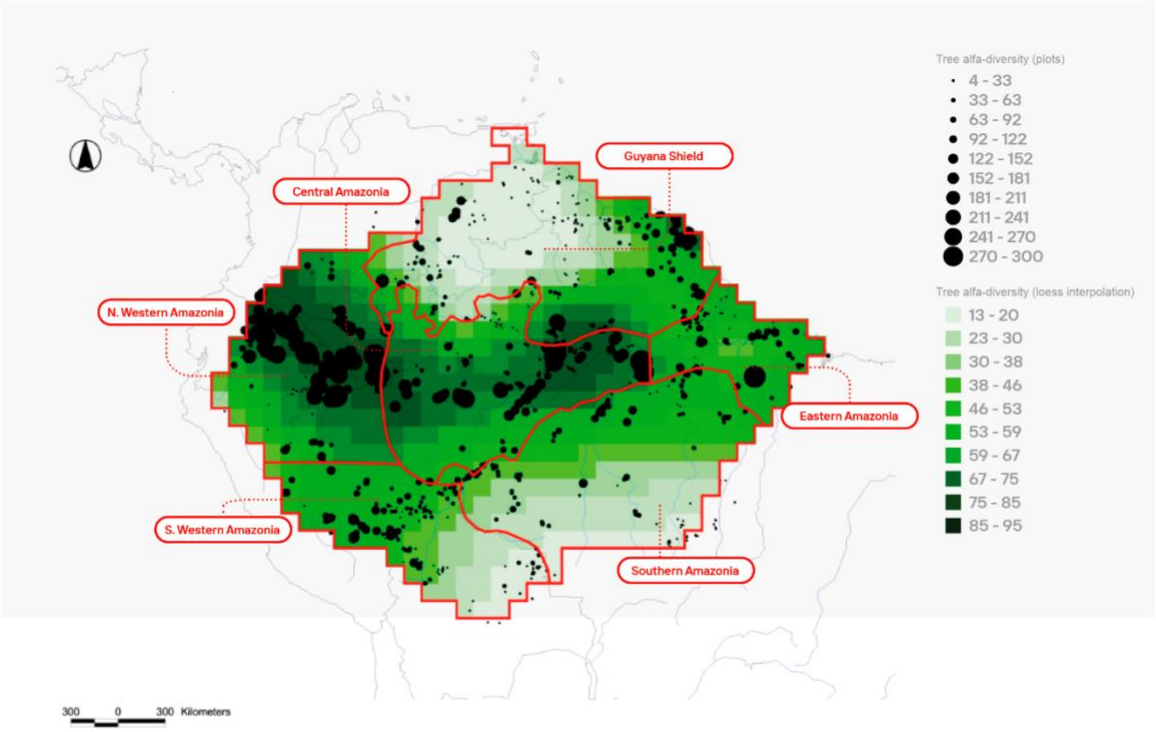


Figure 4.03. Map of tree α-diversity of the Amazon (http://atdn.myspecies.info), based on an interpolation of Fisher's α of 2282 plots of mostly 1-ha. Black dots: Fisher's α of individual plots. Green background color: the interpolated values calculated for 565 Amazonian 1-degree grid cells (~111 km). In gray the six regions of the Amazon as used in this chapter (Quesada et al. 2011, ter Steege et al. 2013).

The Amazonian forest holds approximately 392 billion individual trees with a diameter of over 10 cm (dbh) (ter Steege et al. 2013), amounting to 11% of all trees on earth (Crowther et al. 2015). If trees over 2.5 cm dbh are chosen (Draper et al. 2021) the number of 390 billion may easily double. The average density is approximately 570 individual trees per hectare, with highest densities in the wettest parts, notably NW Amazonia (ter Steege et al. 2003).

The composition of Amazonian forest appears to be determined by two main gradients: soil fertility (ter Steege et al. 2006, Tuomisto et al 2019, Chapter 1), which increases from east to west (Chapter 1) and annual rainfall (ter Steege et al. 2006, Esquivel Muelbert et al. 2016), which decreases from NW Amazonia towards Southern Amazonia (see Chapter 5), where the forest gradually changes into cerrado (a tree savanna).

Cardoso et al (2017) recorded 14,003 species, 1,788 genera, and 188 families of seed plants in Amazonian lowland rain forest, with one-half of these trees that can reach ≥10 cm DBH (6,727 species, 48% of the total flora; 803 genera, 45% of the total genera). More than one-half of seed plant species diversity in the Amazonian rain forests comprises shrubs, small trees, lianas, vines, and herbs (7,276 species, 52% of total flora). Three of these top 10 families are exclusively herbaceous (Araceae, Orchidaceae, and Poaceae, except for bamboos such as *Guadua* species). Ter Steege et al (2013, 2020) estimated that Amazonia may hold close to 16,000 tree species from an estimated total flora that ranges from 15,000 to 55,000 species, 10,000 of which have been collected in the area (ter Steege et al. 2016, ter Steege et al. 2019b). True Amazonian species may be less in numbers but in the edges of Amazonia many species from cerrado or higher elevations in the Andes can be found, which may explain the difference with the estimate of Cardoso et al. (ter Steege et al 2020). Various species of diurnal and nocturnal tree monkeys, Giant Armadillo (*Priodontes maximus*), Collared Peccary (*Dicotyles tajacu*), Jaguar (*Panthera onca*), South American tapir (*Tapirus terrestris*), Harpy eagle (*Harpia harpyja*), Sloths (*Bradypus* spp.), the Agouti Rat (*Dasyprocta punctata*) inhabit Amazonian forests, as well as a large number of species of amphibians and snakes.

A little over 200 species (out of the estimated 16,000) account for 50% of all trees over 10 cm dbh in Amazonia (ter Steege et al. 2013, ter Steege et al. 2020). From mathematical models it can be estimated that over 10,000 species have less than 1 million individuals in Amazonia, while over 5000 are expected to have less than 5000 individuals. Amazonia thus combines hyper-diversity with hyper-dominance and hyper-rarity.

Ten families contribute 65% of all trees in the Amazon, Fabaceae (47 billion), Arecaceae (26 billion), and Lecythidaceae (20 billion) being the most abundant. The ten most abundant species in all of Amazonia are *Eschweilera coriacea* (4.7 billion), *Euterpe precatoria* (3.9 billion), *Oenocarpus bataua* (2.8 billion), *Pseudolmedia laevis* (2.8 billion), *Protium altissimum* (2.8 billion), *Iriartea deltoidea* (2.6 billion), *Mauritia flexuosa* (1.9 billion), *Socratea exorrhiza* (1.9 billion), *Astrocaryum murumuru* (1.8 billion), *Pentaclethra macroloba* (1.7 billion) (ter Steege et al. 2020). It is interesting to note that palms (Arecaceae) are the second most abundant family in Amazonia and contribute seven of the ten most abundant species and do so with very few species compared to the most abundant family, Fabaceae. The latter have 789 species in the plot data of ter Steege et al. (2020), while Arecaceae have only 74. In fact, Arecaceae are five times more likely to be among the ~220 hyperdominants than would be expected on the basis of its species richness. Fabaceae are also the family with the highest tree species richness in Amazonia with 1386 collected species (ter Steege et al. 2019b), For all seed plants the majority of the species rich families are small statured or herbaceous, except Fabaceae (Cardoso et al. 2017).

Tree species diversity is not evenly distributed across Amazonia (**Figure 4.03**). The highest diversity is found in northwestern Amazonia and central Amazonia where single plots of one hectare may have over 300 tree species (Amaral et al. 2000, Gentry 1988). Much lower diversity is found on Brazilian and Guayana shields, especially towards the edges of the Amazonian forest.

Species richness is highest in Dryland (terra firme) forests (**Figure 4.04**), especially those of the more fertile western Amazonia, and lowest in flooded forests (VA - várzea, IG - Igapó), swamp forest (SW) and white sands (PZ). Although fertility and flooding may affect species richness, we strongly believe that tree diversity (and the inverse – dominance) is strongly linked to the area a particular system makes up in Amazonia (ter Steege et al. 2000, ter Steege et al. 2019a).

2.1.2. White sand forests

White sand forests (known by common names like campinarana, Amazonian caatinga, Varillal) are found on pockets of highly leached deposits of podzolized white-sand (Adeney et al., 2016). White sand forests occupy roughly 3-5% of Amazonia with major occurrence in the upper Rio Negro area and the Guianas (Adeney et al., 2016). They are generally species poor, especially in the Guianas, a feature often attributed to their nutrient poorness but more likely a consequence of their small, fragmented area (ter Steege et al. 2000, 2019a). Because of the stark soil differences between white sand forests and terra firme forests, white sand forests are characterized by high levels of endemism (Adeney et al., 2016). Tree genera typically found in white sand forests include *Eperua*, *Micrandra, Clathrotropis, Dicymbe, Hevea*, *Aspidosperma, Protium*, *Licania*, *Pouteria*, *Swartzia* (ter Steege et al. 2013). Impoverished areas (often due to burning) tend to become a more scrub-like vegetation (locally called bana, muri scrub), often dominated by *Humiria balsamifera* and in the Guianas by *Dimorphandra conjugata* as well (Lindeman & Molenaar 1959). Because of their isolation in small patches, white sand forests may never recover species that have been lost (Álvarez

Alonso et al. 2013). White-sand ecosystems in the central Amazon still remain inaccessible and poorly studied (Adeney et al., 2016).

2.1.3. Savannas and grasslands

Savanna vegetation is characterised by presence of trees up to 40% cover, often less than 8 m tall, with a graminoid layer. Savanna occupies 14% of the Amazon basin (including Tocantins-Araguaia basin) and is distributed in terra firme in southeast of Brazilian Amazonia, and in permanently or seasonally flooded sites, as in Beni savanna in Bolivia, in patches of open savanna under washed white sand across Amazonia, or on degraded lands subject to fire. White sand savannas are mainly found in the upper Rio Negro area and the Guianas (see above).

Savannas extend over sandy-clay substrates and eventually form forest islands - around 0.3 to 1.5 km^2 - mixed with swamps in depressions and gallery forests within the basin, which are part of the drainage system of the whole landscape. Woody savannas on *terra firme* or slighty higher-relief terraces of the alluvial plain are formations with species of *Curatella americana, Anacardium microcarpum, Hancornia speciosa, Qualea grandiflora, Byrsonima crassifolia, Tabebuia* spp., as well as grasses: such as *Trachypogon, Paspalum*, Cyperaceae and others (Pires and Prance 1985). Among the animal species characteristic of the savannas are the White-Tailed Deer (*Odocoileus virginianus*), Greater rhea (*Rhea americana*), Southern screamer (*Chauna torquata*), Banded armadillo (*Dasypus novemcinctus*), and craned wolf (*Crysocyon brachyurus*).

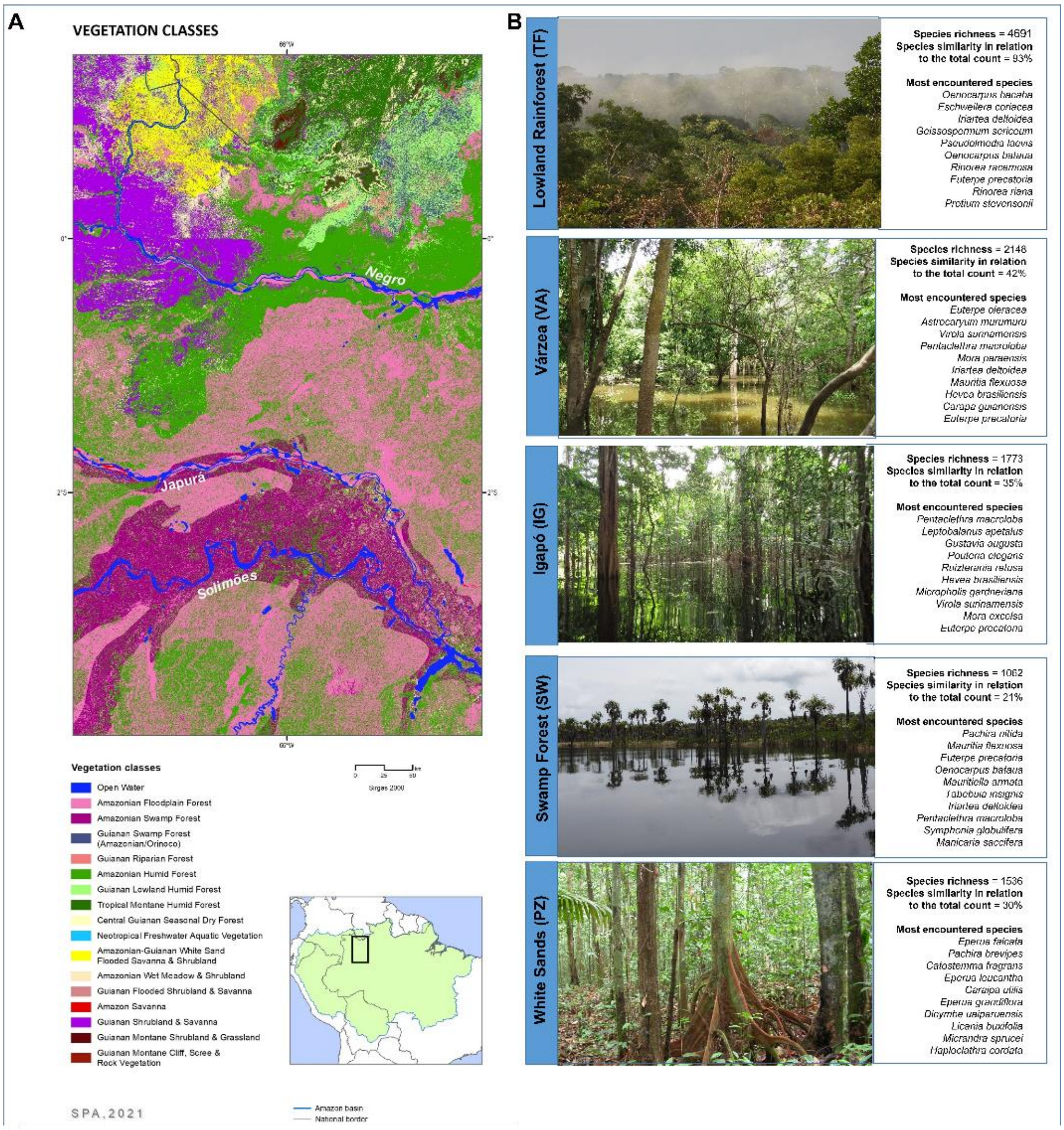


Figure 4.04. **A**. Key ecosystems are found in the Amazonia lowland rainforest, such as Floodplain Forests, Amazon Savanna, White-Sand Savanna, and Seasonally Dry Forest. B. The ten most encountered tree species on ~2000 plots across Amazonia by forest type (IG – igapó, PZ – white sand forest; SW – swamp forest; TF – terra firme forest; VA – várzea forest. Top lines: total species encountered in plots in these forest sytems and the percentage compared to the 5058 species in all 2000 plots (data: ter Steege et al 2015).

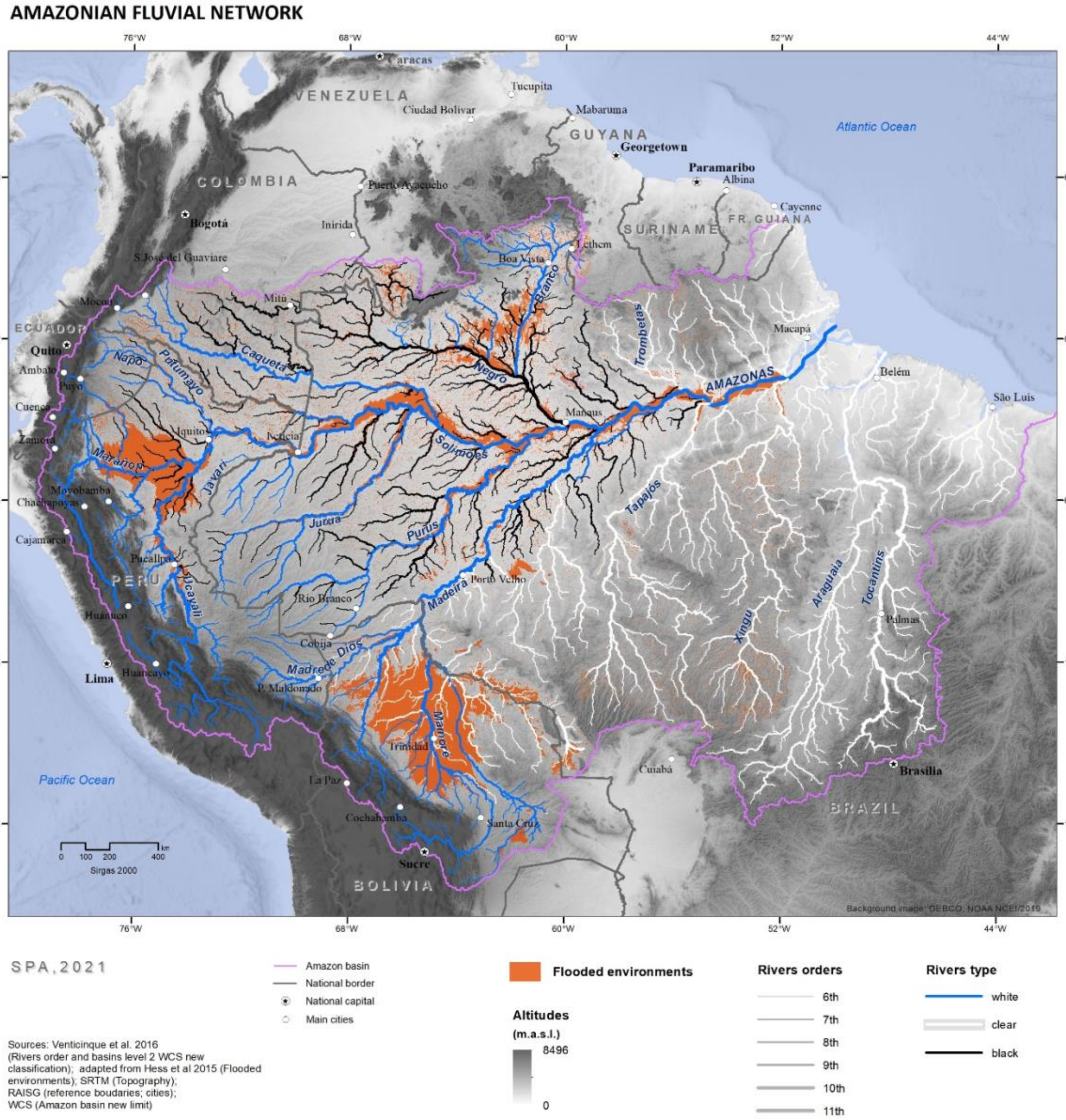
2.2. Fresh Water bodies and Wetlands

Freshwater ecosystems in the lowland basin (lower elevation than 500m) 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, flooded forests, and marshes. These ecosystems are a fundamental part of the large fluvial system of the Amazon and occupy 800,000 km^2, or 14% of the drainage area (Hess and Melack 2011). Aquatic ecosystems in the Amazon are connected through the annual *flood pulse*, the periodic fluctuation in water level that connects lowland rivers with their floodplain and allow the exchange of water, organic and inorganic materials, and organisms (Junk and Wantzen 2003, Junk et al., 2015; see 3.2 below). Depending upon classification criteria (e.g., scale, floristic composition, geomorphology, the pattern of inundation, and water chemistry), aquatic ecosystems and freshwater wetlands may vary from a few general types to more than 30 distinctive ecosystems (Comer *et al.* 2020).

2.2.1. Rivers, Lakes & Forest streams

The Amazon drainage basin is formed by the Amazon River and approximately 15, 269 sub-basin tributaries with catchment areas between 300-1,000 km^2 (Venticinque et al., 2016). The largest tributary systems that join the Amazon are the Madeira, Negro, Japurá, Tapajos, Purus and other rivers that are among the 20 largest rivers on the planet. With more than 7,000,000 km^2, the Amazon is the most extensive hydrographic network in the world, bordered by riparian forests or swamps, and sustains the greatest freshwater fish diversity on Earth; an ichthyofauna that is equivalent to 15% of all freshwater species currently described (Junk et al., 2011, Tedesco et al., 2017). In the animal communities associated with aquatic ecosystems there are numerous species of fishes, the Capybara (*Hydrochoerus hydrochaeris*), Neotropical otter (*Lutra longicaudis*), Amazon River Dolphins (*Inia* spp.), Yellow-Spotted River Turtle (*Podocnemis unifilis*), Matamata (*Chelus fimbriatus*), Anaconda (*Eunectes murinus*), Black Caiman (*Melanosuchus niger*), and other species of crocodilians, among others.

The Amazonian fluvial network is made up of different types of waters (**Figure 4.05)**. Amazonian rivers are generally classified into white-water, clear-water, and black-water, based on the color of the water, which is related to transparency, acidity (pH), and electrical conductivity (Sioli 1984, Bogota-Gregory et al, 2020, **Table 4.01**). These water characteristics also are correlated to the geological and geomorphological properties of the river catchments and their origins (McClain and Naiman 2008). The properties of the catchment directly influence the composition and the amount of suspended sediments in the water and, in turn, the productivity of rivers and floodplain lakes (Sioli 1984). The fish communities in rivers and associated floodplains also are influenced by water characteristics. Conductivity and turbidity in particular, seem to be major drivers shaping Amazonian fish communities (Bogota-Gregory et al, 2020).



Sources: Venticinque et al. 2016 (Rivers order and basins level 2 WCS new classification); adapted from Hess et al 2015 (Flooded environments); SRTM (Topography); RAISG (reference boudaries; cities); WCS (Amazon basin new limit)

Figure 4.05. Amazon River Network across the largest tributary systems and the entire Amazon Basin (source: Venticinque et al. 2016), indicating distribution of flooded environments (modified from Hess et al. 2015). Wetland areas cover ~14 % of the total basin (5.83×10^6 km^2) and 17 % of the lowland basin (5.06×10^6 km^2) (Hess et al. 2015).

Table 4.01. Ranges of physico-chemical properties in blackwater, clearwater, and whitewater for rivers and floodplain lakes across the basin (gray text) (source: Bogotá-Gregory et al. 2020). EC conductivity, DOC dissolved organic carbon, DO dissolved oxygen, Inorg. Inorganic, Herb. herbaceous

Water Chemistry	Whitewater	Clearwater	Blackwater
pH	High (6.5-7.5) (near neutral)	Intermediate (EC 5.5-8.0)	Low (3.5-6.0) (acidic)
Color	Turbid, Cafe con Leche	Clear or blue-greenish	Reddish or brownish
Nutrient	High (EC 40-300 µS cm^{-1})	Low (EC 5-40 µS cm^{-1})	Low (EC 5-20 µS cm^{-1})
Dominant cations	Na^+/K^+	Variable	Ca^{2+}/Mg^{2+}
Dominant anions	$CO_3{}^{2-}/NO_3{}^{-}/PO_4{}^{3-}$	Variable	$SO_4{}^{2-}/ Cl^-$
DOC	High	Low	High
Transparency	Low (0.1-0.6 [usually < 0.3] m)	High (1-3 m)	High (0.6-4 m)
	Variable (LW <0.6, HW 0.5-3 m)[b]		
DO[a]	High (2-8 mg L-1)	High (2-8 mg L-1)	High (2-8 mg L-1)
	Variable (LW[c] 2-8, HW[c] 0-3 mg L^{-1})		
Temperature	High (29-32°C)	High (29-32°C)	High (29-32°C)
	Variable (LW 29-34, HW 27-32 °C)[d]		
Inorg. sediment load	High	Low	Low
Sediment type	Fine alluvial silt	Sand	Sand
Sediment fertility	High	Low	Low
Herb. macrophytes	Absent-Sparse	Absent-Sparse	Absent-Sparse
Floodplain forest	Várzea (high-productivity)	Igapó (intermediate-productivity)	Igapó (low-productivity)

. [a] Periodic phytoplankton (including cyanobacteria) blooms induce DO supersaturation (ca. 8–15 mg L^{-1}) and color clearwater green. [b]Precipitation of suspended silt due to reduced flow in white water floodplain lakes substantially increases transparency relative to parent white water river. [c]High water hypoxia results from litter decomposition in inundation forests; this effect is greater in large white-water floodplains. [d]Shallow white water lakes reach extreme high low-water temperatures.

White-water rivers (such as the Amazon main stem, the Juruá, Caquetá-Japurá, Purus, Marañón, Ucayali, and Madeira) originate in the Andes. The Andean mountains supply most of the terrestrial sediments, organic matter and mineral nutrients influencing the hydrology, geomorphology, biochemistry, ecology and productivity of white-water rivers and their floodplains, all the way to the Amazon River estuary, associated mangroves, and to the ocean (McClain & Naiman 2008; Filizola & Guyot 2009; Encalada et al. 2019). Andean-derived large sediment loads control downstream channel erosion and width, bed elevations, and the availability of riparian habitats and vegetation. These in turn influence the connectivity between river channels and floodplains, and therefore spatial patterns of inundation and floodplain productivity (Constantine et al. 2014; Forsberg et al. 2017). White-water rivers are turbid, with water transparency ranging between 20 and 60 cm, because the high sediments loads contain suspended clay particles from drained soil and completely degraded plant material. White-water rivers have near-neutral pH and the relatively high concentration of dissolved solids is reflected by the electric conductivity that varies between 40–300 μS/cm (McClain and Naiman 2008, Bogota-Gregory et al. 2020). White-water rivers are surrounded by diverse várzea floodplain forests and extensive floating meadow wetlands (Wittmann et al, 2011, see 2.2.2. below).

Clear-water rivers (such as the Tapajós and Xingu Rivers) have their upper catchments in the cerrado region of the Central Brazilian and drain the ancient Brazilian shield which has been strongly eroded over millenia (Sioli 1984). The pH of clear-water rivers varies from acidic to neutral, depending on the soil, and the water hardly carries any suspended and dissolved solids (Sioli 1984). The transparency of their greenish waters is high (100–300 cm), electrical conductivity ranges between 5–40 μS cm, and pH varies between 5.5–8 in large rivers (Bogota-Gregory et al. 2020).

Black-water rivers have their origin in lowlands, are translucent, high in dissolved organic carbon, and low in nutrients. Rivers such as the Negro in Brazil and Vaupés and Apaporis in Colombia drain the Precambrian Guayana shield, which is characterized by large areas of white sands (podzols). Water transparency ranges between 60–400 cm, with low quantities of suspended matter but high amounts of humic acids (rich in dissolved organic carbon (DOC) from the incomplete degradation of forest plant material), which give the water a brownish-reddish color. The pH values are in the range of 3.5–6 and electrical conductivity varies between 5–20 µS/cm (Bogota-Gregory et al. 2020). Clear and black water rivers are surrounded by another type of flooded forest, igapó (See 2.2.2. below for a detailed description of Amazonian floodplain wetlands).

Many rivers and streams do not fit in these three classic categories and must be considered as “mixed waters”. Greater variability in water biochemistry results from the influence of lower order tributaries with different biogeochemical water properties that vary seasonally depending on flooding levels and connectivity.

Amazonian lakes are the result of fluvial processes in depressions or flooded valleys; four main categories are distinguished: 1) lagoons in ancient lands not directly related to river systems (e.g., Hill of Six Lakes in northern Amazonia), 2) lakes in river valleys and quaternary sediments (not related to geographical features: e.g., Pará and Rondonia states), 3) lakes generated by river processes (e.g., Boa Vista Formation, northern Amazon), and 4) "lakes" of wetlands (a mosaic of lakes with large diversity in origin, shape, and functioning) (Latrubesse 2012). Depending on fluvial processes, two further groups are recognized: 1) lagoons formed by the lateral displacement of the channel, in stretches of abandoned channels and meanders (lagoons or swamps depending on the degree of sedimentation), and lagoons that join islands to the floodplain; and 2) lakes generated by geographical features such as those built by vertical accretion processes in the main channel and by floods in the alluvial plain (e.g., square lagoons also influenced by tectonics in SW Amazonia), or by deltas of alluvial plains, with dikes and blocked valleys (e.g., ria lakes).

In meandering rivers such as those found in the Amazon basin, sediment deposits rich in clay form within floodplains. These clay deposits slow water flow and thus help to decrease the migration rates of the channel – up and down streams – affecting bank erodibility on a large scale (10– 50 km) and sinuosity by 30% (Schwendel et al. 2015). The grain size of clay-rich sediment deposits is similar to that of deposits near the outlet of a meandering lake (1.5–3.0 μm) and form clay plugs (Gautier et al. 2010). The abandoned meanders of rivers are known as oxbow lakes that may or may not recover the sinuosity of the river. However, while stagnant waters remain, aquatic submerged plant communities rapidly colonize floodplain lakes, including species such as *Victoria amazonica, Lemna* spp.*, Nymphaea gardneriana,* and *Eichhornia* spp., among others. Oxbow lakes of black-water rivers are typically free of aquatic plant communities due to their low nutrient levels.

Few areas within lowland Amazonia are more than 100 m above the river, where water comes to the surface in the form of a dense network of small streams. Most of the stream fauna depends on energy inputs from the surrounding forest (e.g, insects and plant material) and much of the terrestrial flora and fauna also depend on resources from streams. This intricate connection between aquatic and terrestrial ecosystems continues as the streams coalesce to form larger rivers. In general, small streams are considered part of the terra-firme forest ecosystem and harbor great aquatic biodiversity (Arbelaez et al. 2008). However, as they form larger rivers, the forest-canopy is no longer continuous, instead the floodplain areas around rivers support extensive forests (see 2.2.2. below), and the terrestrial and aquatic ecosystems become more distinct (see 3.2. below).

2.2.2. Freshwater Wetlands

There are several definitions of wetlands, but a broad and simple definition for wetlands is the one proposed by Junk et al. (2011, 2014) which states that **“wetlands are ecosystems at the interface between aquatic and terrestrial environments with biota adapted for life in water or in water-saturated soils.”**. Recent large-scale mapping efforts have identified numerous wetlands dominated by vegetation, in different sub-basins of the entire Amazon basin. According to Junk et al. (2011) wetlands cover an extensive area of 2.1 million km^2 and are divided into two main groups: 1) those with relatively stable water levels (e.g., *Mauritia flexuosa* palm swamps), and 2) those with oscillating water levels (e.g., floodplain forests, mangroves). Some of these wetlands are forest-dominated and broadly distributed while others are emblematic as they represent specific regions within the basin, such as savanna ecosystems in the Llanos de Moxos, located in the Madeira basin of Bolivia; Bananal savannas of Brazil which are seasonally inundated grasslands, sedgelands, and open woodlands; among many others (Castello et al. 2012, **Figure 4.01**). In the Upper Negro river basin, the Amazonas Savannahs Refuge and parts of the Imeri Refuge are considered centers of endemism for floodplain tree species, such as *Mauritia carana*, *Ocotea esmeraldana*, and *Vitex calothyrsa* (Junk et al., 2010). All of these wetlands are vital to support local communities' livelihoods.

Floodplain Forest

Seasonally flooded forests are second in area compared to terra-firme forests (0.76 million km^2, 13%), and subjected to predictable, long-lasting, annual flood pulses (Junk et al., 2011; also see 3.2. below). These forests are flooded due to their low topographic location and poorly drained soils. Flooding may last up to six months and water level may fluctuate up to

10 m between the dry and flood seasons (Schöngart and Junk 2007) and the timing, duration and magnitude is variable across the basin. Such temporal and spatial variation is mostly driven by air circulation patterns and headwater precipitation modulated by the Intertropical Convergence Zone and topography (Siddiqui et al., 2021). Although these forests are annually flooded, different floristic zones are distinguished which are influenced by the input of sediments and nutrients in river waters, flood regimes, and hydro-geomorphic dynamics (Prance 1979, Wittmann 2010).

Floodplain forests along white-water rivers are known as *várzea* in Brazil (or *rebalse* in Colombia) and represent the most extensive type of flooded forest in South America, covering approximately 456,300 km^2 of the Amazon basin (Junk and Wittmann, 2017). Amazonian white-water river floodplain forests contain around 1,000 species of trees, making them the most diverse floodplain forests in the world (Ferreira & Prance 1998; Wittmann et al. 2002, 2006). A significant number of tree species almost are completely restricted to the floodplain (~40% of the most common central Amazonian várzea tree species), while only ~31% of tree species in várzea are shared with terra firme forest (Wittmann et al. 2011). Due to the seasonal influx of nutrients carried by white-water rivers, floodplain forests are eutrophic and highly productive (Junk & Piedade 1993), but their flora and fauna diversity is less than that of terra firme forest (Patton et al. 2000; Haugaasen & Peres 2005a, b). This is because of the selective pressure imposed by prolonged annual floods. Due to its high productivity, várzeas have been important centers of human colonization which has intensified in the last thirty years (Piedade et al. 2010). Data on Amazon aquatic ecosystem productivity are relatively few but those available show that remarkably high values are locally possible. This is likely to be due to the combination of abundant nutrient and water supply, and insolation, and macrophytes adapted to rapidly occupy the water-atmosphere interface when conditions permit (**Table 4.02)**. Floodplain forests of Brazil, Peru and Ecuador are characterized by the presence of families such as Fabaceae, Moraceae, Arecaceae, Lecythidaceae and Annonaceae (Nebel et al. 2001) and the flooded period may vary from 1 or 2 months to 6 months. In varzeas of the central Amazon, characteristic tree species include *Ceiba pentandra, Hura crepitans, Nectandra amazonum,* and *Cecropia* spp. (Worbes 1997). These species represent the early sequence forest species, have low wood density, and make up the successional process which is governed by hydrological seasonality. Tree density (at 10 cm dbh) in várzea varies along successional stages and flood-gradient position (i.e., high and low varzeas), being in average 400–500 individuals ha^{-1} and with highest values occurring in early-secondary stages (800–1,000 individuals ha^{-1}) (Wittmann et al., 2011).

Table 4.02. Net primary production (NPP, dry weight) for the most important populations and communities of aquatic herbaceous plants in central Amazon várzea. NPP was measured under different methods and assumed to have a monthly loss between 10 and 25% of the biomass (source: Piedade et al. 2010).

Population/Community	Maximum NPP (t.ha^{-1})	Time for production (months)
Monospecific stands of *Echinochloa polystachya* (Kunth) Hitchock[1]	100	12
Monospecific stands of *Paspalum fasciculatum* Willd.[2]	70	7.7
Mixed populations dominated by *Hymenachnea amplexicaulis* (Ruudge) Nees[2]	48	9.5
Monospecific stands of *Paspalum repens* P.J. Bergius[2]	33	4
Monospecific stands of *Oryza perennis* Moench[2]	27	4
Mixed populations dominated by *Oryza perennis* Moench[2]	17.5	5

[1] Piedade et al 1991; [2] Junk & Piedade 1993.

There are also floodplain forests along black water rivers (Junk et al. 2011), called Igapó in Brazil. The Igapó forests are seasonally flooded by black (or clear) water rivers, for up to 9 m in depth, and cover around 302,000 km^2 (Melack & Hess, 2010; Junk et al., 2011). Due to the lack of soil nutrients, tree abundance and biomass in igapó forests is much lower than in várzea and terra-firme forests (Ferreira 1997, Junk et al. 2015, Wittman & Junk 2017). Montero et al. (2014) recorded 6,126 trees with 243 species, 136 genera, and 48 families in 10 hectares along the middle Rio Negro. Most species found in igapó also occur in other ecosystems, such as terra firme and várzea forests, savanna, swamps, or white-sand forests (Junk et al. 2015). Among herbs, fifty-five species have been documented, belonging to 20 families (Lopes et al. 2008); most of the species were found with an exclusively terrestrial habit in the igapó and belong to two main families: Cyperaceae (45% of the total) and Poaceae (7.3%) (Piedade et al. 2010).

In general, comparison between terra firme, várzea and igapó forests show differences in tree richness (**Figure 4.04**) and structural trends in number of individuals. In general, terra firme forest shows greater density and richness of large trees (diameter at breast height ≥ 90 cm), followed by várzea and igapó forests.

Permanently Flooded Swamps

Permanently flooded or waterlogged areas (swamps) occupy a small area compared to other ecosystems in Amazonia (80,000 km^2, 1%). The extensive palm formations of *Mauritia flexuosa* (buritizal), *Oenocarpus bataua, and Euterpe oleracea* (açaizal) (Arecaceae) are very characteristic of swamps of Amazonia. Their distribution is azonal as they are found from the lowland plain to the Andean foothills, up to 500 m of altitude, always associated with highly stagnant black waters (Moraes et al. 2020), such as in permanent wet depressions within the savanna landscape (*Mauritia flexuosa*) (Junk et al., 2010). There are also permanent swamp areas with rooted plants in channels or depressions within the alluvial plain, characterized by herbaceous species including *Cyperus giganteum, Thalia geniculata, Pontederia* spp., *Eichornia* spp., among others (Pires & Prance 1985; Beck & Moraes 1997).

Flooded Savanna

The seasonally flooded savannas of the alluvial plain cover an area of ca. 200.000 km^2 (Pires & Prance 1985) and represent 6% of flooded plant communities (Meirelles 2006). They occur in northern (Roraima and Rupununi) and southern (Beni savanna) Amazonia, along the Cerrado belts in Brazil and the Guianas, and have strong climatic seasonality (several dry moths) (Junk et al., 2011).

Flooding is mainly influenced by rainfall and the overflow of rivers during 3-5 months, but in a matter of hours the flooding percolates and the landscape returns to its natural state without permanent water, except in lower places and in depressions linked to rivers. On alluvial plains of white-water rivers, Poaceae species predominate (32% of the total), followed by Cyperaceae (20%) (Junk and Piedade 1993), and their contribution to Net Primary Production (NPP) make them the most important aquatic herbaceous plant community (Piedade et al. 2010).

Flooded savannas and grasslands are very fragile ecosystems. Savannization processes are being generated by the reduction of floodplain forests due to various dynamics, such as deforestation and fires driven by severe droughts in minimally flooded regions. Such ecosystem shifts favor grasslands and deteriorated aquatic communities, as was demonstrated in the Pantanal which is considered a hiperseasonal savanna (Nunes da Cunha & Junk 2004).

Mangroves

Mangroves occupy relatively small areas in a narrow littoral belt towards the Atlantic Ocean and in the Amazon estuary. Mangroves are subject to flooding by salt water or brackish water and have only a few tree species, and generally uniform in structure, not exceeding 10 m in height. The dominant mangrove species (in order of abundance) are *Rhizophora mangle* (common names are mangue verdadeiro in Brazil, red mangrove elsewhere), *Avicennia nitida*, and *Laguncularia racemosa* (Pires & Prance 1985, Junk et al 2010). Brazilian mangroves occur mostly along the coasts of Amapá, Pará, and Maranhão states and cover an area of about 11,000 km^2 (ICMBio 2010). The largest mangrove area extends southward from Belém and measures at least 7,000 km^2 (Kjerfve et al. 2001; FAO 2007). Little is known about the wetlands along the coastline north of Belém. For Guyana, Huber et al. (1995) estimated that there are about 900 km^2 of coastal mangroves. In areas with very strong freshwater influence near the Atlantic coast, várzea forests may replace mangroves.

3. ECOSYSTEM FUNCTIONING

3.1. Primary productivity, nutrients, forest dynamics and decomposition

3.1.1. Terrestrial ecosystems

In Amazonia, climatic factors exert the greatest influence on gross production (GPP) in terrestrial ecosystems but a wide range of other factors related to soil, forest disturbance and species composition are also influential in determining how captured carbon is allocated and how long it is stored in tree woody biomass and other ecosystem compartments. Thus, bottom-up studies of the carbon budget and its seasonal variation using intensive measurements in plots of the GEM (Global Ecosystems Monitoring) network (Malhi et al. 2021) show variation in GPP between sites from around 33 to 38 Mg C ha^{-1} year^{-1} for more humid forests (in the west and north) to lower values of 25 to 30 Mg C ha^{-1} year^{-1} in drier forests of the Brazilian Shield and central Amazonia (Malhi et al 2015). However, carbon-use efficiency (CUE), defined as the fraction of fixed carbon that is used to produce plant matter, i.e. NPP divided by GPP, appears to be lower (0.3 – 0.4) in the wetter sites than in more seasonal Amazonia (0.4 – 0.5). Overall, the decline in GPP in the drier sites is compensated by shifts in CUE and in allocation, so that in these studies there is often no clear decline in tree woody growth toward more seasonal parts of Amazonia. Compensatory shifts in CUE and allocation unrelated to climate thereby may effectively decouple spatial variation in GPP, NPP and woody growth.

Less intensive but more extensive measurements of woody growth (**Box 1**) and tree mortality, combined with species composition and soil measurements help confirm the role of non-climatic factors in affecting how carbon is allocated in Amazon ecosystems. In the widespread RAINFOR forest inventories, above-ground woody production is more closely linked to edaphic factors such as phosphorus concentrations than to climate (e.g., Quesada et al. 2012). Other non-climate factors play a role too. Notably, the high tree mortality rates of some Amazon forests as a result of wind-disturbance (e.g., Esquivel Muelbert et al. 2020) and the poor physical structure and relatively shallow rooting depths of many western Amazon soils (Quesada et al. 2012), ensure that more forest here is naturally in early to intermediate successional states, which tend to produce wood faster and may have greater carbon use efficiencies (Rödig et al 2018). Additionally, the nature of the species present makes a difference too - where tree phylogenetic diversity is greatest, forests have greater levels of woody productivity, even accounting for covarying climate and edaphic factors (de Souza et al. 2019). There is also evidence that animals may increase nutrient cycling and subsequently the productivity of the forest (e.g., Sobral et al. 2017), and it is possible that the pre-Colombian extinction of Amazon megafauna has impacted productivity negatively by slowing the nutrient transfer from richer floodplains to hinterland terra firme forests, a function which the original large herbivores would have performed (Doughty et al. 2016).

What does all this mean for forest dynamics, biomass and carbon storage? Inventory plots show that differences in above-ground biomass track more closely to underlying edaphic factors than to climate factors. Mortality rates vary greatly across the Amazon, being higher in the western and southern regions, around 2.2 to 2.8% per year, than in northern and eastern central regions where 1.1 to 1.5% per year is typical (Phillips et al. 2004, Marimon et al. 2014, Esquivel et al. 2020), with the fast turnover forests often corresponding to where soils are relatively rich chemically but offer poor structural support physically. Associated with these high rates of stand-level tree mortality is the prevalence of species with ‘live-fast-die-young’ life-history strategies that tend to favour growth over survivorship, with lower wood density so storing less carbon (Baker et al. 2004, ter Steege et al. 2006, Honorio Coronado et al. 2009, Patiño et al. 2009). Remarkably, basal-area weighted wood density in the slow-turnover forests of the northeast Amazon is up to 50% greater than in fast-turnover forests in the south and west (Phillips et al. 2019). In sum, three decades of careful observation in permanent plots shows that spatial variation in Amazon biomass carbon stocks and dynamics are driven more by soil conditions than climate, and more by spatial variation in mortality than productivity. These findings run counter to the dominant paradigm in ecosystem vegetation models which has emphasised the role of climate and processes of carbon *production* (GPP, NPP, tree growth), rather than its turnover and *loss* (especially mortality) and which often ignore the physical constraints and floristic compositional factors which turn out to largely determine Amazon forest biomass.

The key effects of soils on Amazon ecosystem function extend also to animals and their important functions, including herbivory and seed dispersal. Travellers from the west to the east of Amazonia are often struck by the remarkably low level of insect activity, which can make fieldwork much more comfortable. This likely reflects fundamental controls of cations and other nutrients on the metabolism of animal consumers (e.g., Kaspari et al. 2009) as well as plant producers (e.g. Lloyd et al. 2015). In the white sand forests of the Amazon, it was found that the interaction of impoverished soils and herbivory selects defense mechanisms of the plants, while in those forest formations with clay soils species are rather favored through rapid growth (Fine et al. 2006). Large animals too respond to bottom-up soil controls – for example Stevenson et al. (2016) found that Neotropical primate abundance and diversity are largely controlled by fruit production, and with much greater biomass and diversity in western Amazonia than in the Guyana and Brazilian Shields. Such effects are likely to extend to many other animal groups as we have known for more than a third-of-a-century that production of flowers and fruits in the neotropics is closely tied with soil nutrient status (Gentry and Emmons 1987).

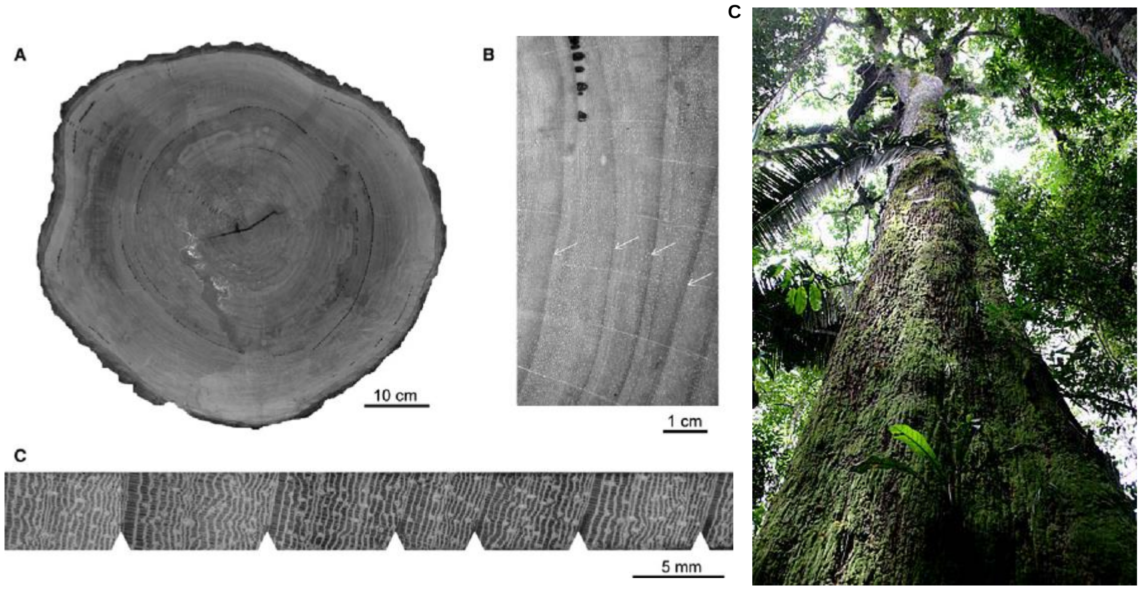
Finally, we note that climate nevertheless does also impact on rates of woody production, and clearly has consequences for forest carbon storage and biodiversity. Both worldwide and in Amazonia, woody production is suppressed in the most extreme seasonal tropical forest climates with high maximum temperatures and high seasonal water deficits (Sullivan et al. 2020). This means that some Amazon forests are already at the climatic limits capable of sustaining productive forest ecosystems. As a consequence, in some tropical forests which have warmed and dried most the long-term carbon sink into mature forest appears to have recently weakened (Hubau et al. 2020). In Amazonia we also know from long-term RAINFOR plots that forest composition is being affected by recent droughts, with the mortality of wet-affiliated genera increasing in places where the dry season has intensified most (Esquivel Muelbert et al. 2019). However not all Amazon forests appear to be so impacted, with large areas with shallow water tables on central and western Amazonia potentially effectively immunized against drought via local water supplies, in some cases even seeing an increase in growth and carbon stocks during recent drought (Sousa et al. 2020). Key areas of scientific uncertainty include the extent to which recent climate change has actually caused the slowdown in the Amazon biomass carbon sink (Brienen et al. 2015) and whether it might now go into reverse with intact Amazon forests becoming a net carbon source with further warming - or whether the shallow water tables and rich biodiversity of so many Amazon forests will help prevent Amazonian forests becoming a net carbon source.

To complete our picture of forest dynamics, we need to understand the decomposition of dead organic material as a fundamental biogeochemical process, both through its role in the forest carbon (C) cycle and, perhaps more importantly, through its role in the recycling of nutrients to soil and plant communities. Any changes in decomposition processes will have profound impacts on the rate and pattern of nutrient cycling, and hence on forest plant and faunal community dynamics. In elevation gradients at the Andes-Amazon interface in Peru, temperature is the variable that best explains variations in litter decomposition rates (Salinas et al. 2011). Pinto et al. 2018 indicate that, as an effect of global change, increases in temperature and dry season duration are anticipated for the southern Amazon Basin and the Pantanal (Gatti, et al. 2014; Junk 2013), so these are likely to induce changes in decomposition rates and patterns. Also, the physiological, morphological, and biochemical characteristics of Amazonian tree species (their functional traits) play an important role in their decomposition. Species type has a large influence on the decomposition rate (k) (Hättenschwiler et al. 2011), most probably through its influence on wood density and leaf quality and morphology. For example, the influence of leaf anatomy is manifested primarily through spongy parenchyma thickness, which strongly influences the moisture-holding capacity of the leaf material, which in turn largely explains the observed moisture content in the leaves.

Box 1. How much does the longevity of Amazonian species vary?

Tree age has generally been inferred based on trunk diameter growth rates (growth rings), mortality (Condit et al. 1995, Shöngart et al. 2015) or radiocarbon dating ($_{14}$C) (Chambers 1989, Vieira et al. 2005). The maximum longevity values based on demographic studies were inferred in 93 species of canopy trees in the rain forest in the Central Amazon, considering the influence of the life cycle - such as wood density, growth form, mortality rate, rate of recruitment, trunk diameter, increase in growth and population density. Maximum longevity ranged from 48 years for the pioneer tree *Pourouma bicolor* (Cecropiaceae) to 981 years for the canopy tree *Pouteria manaosensis* (Sapotaceae), with an overall average of 336 ± 196 years (Laurance et al. 2004). These approximations on the maximum age of the trees coincided with the analyses of the average mortality rates: the longevity of the tree was positively correlated with the density of the wood, the maximum diameter of the stem and the population density, while it was negatively related with annual mortality, recruitment, and growth rates; pioneer species had much shorter longevity than climax trees (Laurance et al. 2004).

Tree age data provide important information for conservation and sustainable forest management. Emergent old-age trees in the central Amazon, for instance, represent a key component of forest's carbon budget, as around 50% of the aboveground biomass is retained in less than the 10% of the largest trees (Chambers et al. 1989). The time spent for a tree to achieve a certain diameter varies with radial growth rates, with the cambial activity being influenced by abiotic site conditions and precipitation that limits water in the dry season (Worbes, 1999). *Bertholletia excelsa* (Lecythidaceae, Castanha-do-Brasil), a tree of 50 m height may have 400 years and a diameter of 150 cm. As growth is higher under favorable light conditions (e.g. under canopy gaps) a tree of 10 cm diameter can have an age varying from 13 to 50 year (Shöngart et al. 2015). The flood tolerant tree, *Calophyllum brasiliense* (Guttiferae, Guanandi), may achieve a maximum age of 490 years in a black-water floodplain. Under permanently waterlogged conditions the longevity is reduced to 72 and 134 years. As consequence, for achieving the 50 cm diameter-cutting limit based on forest management norms in the Brazilian Amazon, *C. brasiliense* would spend 70 years in white-rivers floodplains and about 400 years in black-water floodplains (Rosa et al., 2017), suggesting the adoption of Growth-Oriented Logging to ensure species conservation (Schöngart 2008). The relation between radial growth rates and precipitation in the Amazon floodplain allows an estimate of the effect of climate variability induced by the El Nino phenomenon with forest dynamics. The low precipitation events influenced by El Nino (see Chapter 20) is related to increased growing period of the long-living (143 to 289 years old) hardwood species *Piranhea trifoliata* Baill. (piranheira, Picrodendraceae). Unlike in Terra Firme Forest, the influence of drought on growth rates in the floodplain tree may increase carbon absorption, partially compensating the carbon emitted in terra firme forest under El Niño periods (Shongart et al. 2004). In view of the conservation of the Amazon rainforest, its essential to keep efforts to determine age and growth rate of tropical trees under flooded and non-flooded conditions, and the influence of climate and soil conditions on growing patterns, indispensable information to guide Amazon rainforest wise use and long-term preservation (Vetter and Botosso 1989, Shöngart et al. 2008).



Box-Figure 4.01. (A) Stem disk, and (B) Tree rings of *Bertholletia excelsa* Bonpl. (Lecythidaceae) from a plantation tree in Manaus. Tree rings are defined by an alternating pattern of fiber (dark tissue) and parenchyma (light tissue) (Shongart et al. 2015). (C) *Bertholletia excelsa* achieves 50 meters' height tree in terra firme forests and 400 years of age (Clóvis Miranda/WWF).

3.1.2. Freshwater ecosystems

Like in terrestrial 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 energy and nutrient recycling (Morris 2010). These functions affect and are affected by interactions between living organisms and consecutively sustain biodiversity and human wellbeing. However, unlike terrestrial ecosystems, the flow of water makes aquatic ecosystems highly dynamic in both space and time. This is due to changing physical conditions and biotic components along stream and river channels, from the headwaters to downstream confluence with other rivers or the sea, and the influence of precipitation on streamflow.

The flow of energy and nutrient recycling are prime examples of the dynamic nature of aquatic ecosystems, and Amazonia is no exception. Headwater and forest streams are shaded by vegetation which inhibits algae growth, a key energy producer in aquatic ecosystems. Instead, riparian vegetation subsidizes aquatic food webs that are dominated by shredder invertebrates and decomposer bacteria that help recycle nutrients (Vannote et al. 1980). Nutrients travel downstream in a spiral-like pattern and as the width of the river channel expands downstream, algae growth is no longer limited by shading (Vannote et al. 1980). The lack of dissolved nutrients limits algae production in nutrient-poor rivers such as Amazonian clear-water and black-water rivers, while acidity and low light penetration in dark-stained water further limits productivity in black-water rivers. In turbid white-water rivers, light penetration also is a limiting factor to algae growth (Moreira-Turcq et al. 2003; Dustan 2009). By connecting rivers with floodplain habitats, the *flood pulse* provides a mechanism to compensate for limited in-situ algal productivity by replenishing nutrients during the annual flood (Junk and Wantzen 2003, see 3.2 below).

At a global scale, some wetlands contribute to carbon storage due to the extensive and deep accumulation of below-ground peat deposits. Peat is a type of soil with a top layer composed of at least 50% decomposed or semi decomposed organic material (i.e., 29% carbon content), extending at least 30 cm deep (Gumbricht et al. 2017). Several factors are important at determining the location of peatland ecosystems, including high rainfall, frequent flooding, low drought and fire frequency, and a low-lying topography that creates waterlogging and anoxic conditions for peat accumulation (Draper et al. 2014). Peatland ecosystems also are influenced by different types of waters, with a gradient of nutrient content. They can be nutrient-poor ombrotrophic bogs if they are dominated by atmospheric water, or they can be nutrient-rich swamps that are influenced by rivers (Lähteenoja & Page 2011). For example, in the Pastaza-Marañon foreland basin located in western Amazonia in Peru, an area of 35,600 ± 2,133 km^2 contains 3.14 (0.44–8.15) Pg C below palm swamps, while peatland pole forests represent the most carbon-dense ecosystem (1,391 ± 710 Mg C ha^{-1}) in Amazonia (Draper et al. 2014). The Pastaza-Marañon peat deposits extend 6 m deep, 4 m deeper than initially estimated (Gumbricht et al. 2017). Because peatland ecosystems function as C sinks, they play a key role in maintaining the natural balance of the C cycle, modulating global warming. Recent models estimate that 38% of Amazon wetlands form peat deposits; however, the lack of climate data needed to build hydrological models hinders quantification of the true extent of peatland ecosystems within the Amazon basin, and thus the importance of the region in the global greenhouse gas budgets (Gumbricht et al. 2017).

3.2. The Flood Pulse and Aquatic-Terrestrial Transition Zone

Variation in water flow and depth is driven by regional and local precipitation patterns, which coupled with variations in stream order, latitude, and elevation across the enormous Amazon River basin drainage, create distinctive flow regimes across regions (Goulding et al. 2003, Siddiqui et al. 2021). In a recent classification, Siddiqui and collaborators (2021) identified 6-7 flow regimes, based on a combination of hydrological characteristics that include the timing of the wet season, magnitude of change in streamflow, and number of times streamflow changes from rising to falling within a year. The timing of maximum flow, for instance, changes spatially across the Amazon basin with maximum flooding occurring in February-March in the southern tributaries and in June-July in the northern tributaries. The magnitude of change in streamflow increases in lower elevation areas while at the same time the frequency is reduced to a single large flood episode. Rainfall in the headwaters of large Andean rivers causes a *flood pulse* that travels downstream and leads to a predictable annual hydrological cycle with distinct water-level periods (rising, flood, falling, and dry) and long-lasting flooding (4-15 m in depth and weeks to months in duration) in floodplains of lowland rivers (≤ 500 m asl). This *flood pulse* drives multiple physical, biological, and ecological processes in the Amazon basin, from sediment transport to fish migration. In addition, the *flood pulse* drastically transforms the landscape of lowland rivers by creating an aquatic-terrestrial transition zone (ATTZ) that allows the movement of nutrients and organisms between main river channels and floodplain habitats (Junk & Wantzen 2003).

The interactions between terrestrial and aquatic components are among the most important processes of the Amazonian ecosystem. Floodplain wetlands controlled by the seasonal *flood pulse* of white-water rivers are probably the best-documented examples of the importance of ATTZ in the Amazon basin (Junk et al. 1984). These Amazonian floodplains, which are among the most productive natural systems on earth, originate from the accumulation of large sediment loads drifting from the Andes, fueled by their associated nutrients (Junk et al. 1984; Melack & Forsberg 2001; McClain & Naiman 2008). Complex floodplain macrophyte and forest communities have adapted to these seasonal sediment fluxes and year-round lateral exchanges between the main channel of rivers and their floodplains.

Terrestrial primary production, organic matter and nutrients captured when floodwaters invade the floodplains decompose or are consumed by organisms, becoming the basis of the aquatic food chain for a rich biota (Junk 1984; Junk et al. 1984; Melack & Forsberg 2001). Part of this productivity goes back to the river main stem through the many organisms that move between the floodplains and the river, including large numbers of fishes during massive annual migrations (Goulding 1980, 1993). Floodplains play crucial roles as feeding grounds and nursery areas for many fishes (Lima & Araujo-Lima 2004; Castello et al. 2015, 2019). For instance, most commercially important fishes supporting large fisheries in the Amazon basin are detrivore, herbivore and omnivore species performing annual migrations into the white-water floodplain habitats that largely contribute to their production (Junk et al. 1984; Bayley & Petrere 1989; Bayley 1995; Goulding et al. 1996, 2019; Isaac et al. 2016). In floodplain lakes connected to white-water rivers, the lack of currents allows sediment settling and greater water transparency which facilitates phytoplankton growth that fuels a zooplankton-based food web. Thus, floodplain lakes play a key role as nursery and feeding grounds to juveniles of fish of commercial value (Oliveira 2006). The current consensus among researchers is that a mixture of carbon generated in seasonally available floodplain habitats by algae, forest vegetation, and aquatic plants, plays a pivotal role at subsidizing aquatic food webs and commercial fisheries across Amazonia (Benedito-Cecilio et al. 2000, Santos et al. 2017, Correa & Winemiller 2018).

Massive annual fish migrations also contribute to transfer a small portion of these Andean-derived energy and nutrients from the white-water floodplains to the nutrient-poor black- or clear-water tributaries (see details below). Another perfect illustration of the intimate ecological interactions between the aquatic and terrestrial systems is the ancient mutually beneficial co-evolution and co-adaptation between trees and fishes in Amazonian floodplains. Most tree species fruit during the high-water season, when fish invade the flooded forest (Ferreira et al. 2010; Hawes & Peres 2016). Hundreds of fish species have evolved frugivory habits and may have been the first vertebrate seed dispersers in the Amazon (Goulding 1980; Correa & Winemiller 2014; Correa et al. 2015a). They eat the fruits falling in the water from floodplain trees and disperse their seeds over long distances, improving their germination and thereby contributing to the maintenance of the flooded forest (Goulding 1980; Kubitzki & Ziburski 1994; Waldhoff et al. 1996; Correa et al. 2015a,b). In addition to fruits, fish also consume copious amounts of invertebrates that undergo vertical migrations toward the forest canopy during the flood season. The consumption of leaf-eating insects and carnivorous invertebrates that in turn predate upon leaf-eating insects creates an indirect feeding link between fish and trees. Whether directly or indirectly, flooded forests provide a key terrestrial subsidy to riverine fishes, particulary in nutrient-poor black- or clear-water rivers (Correa and Winemiller 2018).

The flood pulse influences multiple aspects of fish reproductive strategies, including fecundity (number of eggs), age at first reproduction, number of reproductive episodes per year, and parental care (Tedesco et al. 2008). As a result, changes in water level affect fish species differently, the effects on fishing yields can lag over the next 2-3 years. The flood pulse also affects the movement patterns 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. During the dry period, seedling germination drives the movement of terrestrial animals to floodplain forests, while hummingbirds take advantage of the synchronicity in flower production (Haugaasen and Peres 2007, Beja et al. 2009). Moreover, flooding enhances habitat heterogeneity in floodplain forests which influences the formation of unique bird, bat, and amphibian communities not found in adjacent terra firme forests (Beja et al. 2009, Pereira et al. 2009, Ramalho et al. 2018).

4. CONCLUSIONS

The Amazon biogeographical region covers ~7 million km^2, 5.79 km^2 of which are lowland tropical rainforests. We have shown that climate but particularly soil has a strong influence on species richness and composition, and subsequently on forest functioning. Based on geological age of soil material Amazonia can broadly be divided into 6 regions (Figure 4.03).

There is still a strong debate on the species richness of Amazonia. A well supported estimate for trees (dbh > 10 cm) is 16,000, ~10,000 of which have been collected. Estimates of the total flora range from 15,000 – 55,000. As in other tropical areas Fabaceae (bean family) are the most abundant and species rich among the woody species. South America and Amazonia are also renown for its palm abundance and richness.

Amazonia holds the largest tropical wetland system on earth, having 15% of all known fish species (see Chapter 3, Jézéquel *et al.* 2020).

The rivers are classified as white water (rivers carrying sediments from the Andes); clear water (draining the two shield areas); black water (draining the white sand areas). The water type determines the forest type along the rivers, with igapó along sediment-poor clear and black waters and várzea along the white, sediment-rich waters. The physical-chemical characteristics of the different water types, particularly electrical conductivity and turbidity, are major factors shaping fish communities in rivers and associated floodplains. The *flood pulse* causes marked periods of floods and droughts, which drive physical, biological, and ecological processes, from sediment transport to fish migration, and together with the elevational gradients in the floodplain are factors that favor the maintenance of various plant communities. The white-water wetlands are probably the best documented examples of the importance of the aquatic terrestrial transition zone and among the most productive systems on the planet.

Variation in gross primary productivity between forest sites ranges 33 to 38 Mg C ha^{-1} year^{-1} for more humid forests (in the west and north) to lower values of 25 to 30 Mg C ha^{-1} year^{-1} in drier forests of the Brazilian Shield and central Amazonia and is also largely driven by soil characteristics. Climate nevertheless also impacts the rates of wood production, and clearly has consequences for forest carbon storage and biodiversity. Both worldwide and in Amazonia, wood production is suppressed in the most extreme seasonal tropical forest climates with high maximum temperatures and high seasonal water deficits (Sullivan et al. 2020). This means that some Amazon forests are already at the climatic limits capable of sustaining productive forest ecosystems.

5. RECOMMENDATIONS

- Document ecological networks and their implications for maintaining these ecosystems in the long-term to understand the ecological and evolutionary relationships among species and the ecosystems that are truly astounding.
- Conservation initiatives must protect not only forests, but also all the species within them to guarantee ecological functioning. Large areas of forests, savannas and aquatic ecosystems should be maintained to establish large-scale, landscape-level conservation initiatives, that maintain core areas and also maintain connectivity, to provide sufficient security for the survival of wide-range species, migratory species, the innumerable less abundant species, species with patchy distributions, and as many as possible functional traits of different species.
- The connectivity of the ecosystem and landscape processes from the Andes to the Amazon, as well as the interaction with terrestrial and aquatic environments, favors

heterogeneity and consequently natural diversity, and should be preserved by all Amazonian states.

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7. CORE GLOSSARY

Andes. Refers to the Andes mountain range is a chain of mountains in South America between 11° N latitude and 55° S latitude, which crosses Argentina, Bolivia, Chile, Colombia, Ecuador, Peru and part of Venezuela. It is the longest mountain range on Earth, about 7,500 km long.

Aquatic ecosystems. A community of organisms that lives and interacts within an environment that is water. All the system's plants and animals live either in or on that water. The specific setting and type of water, such as a freshwater lake or saltwater marsh, determines which animals and plants live there.

Alluvial plain. Flat surfaces aggraded by meandering, anastomosing, and/or braided river channels, which are bordered by flat-lying areas.

Amazon basin. Or Amazonia is the largest lowland in South America that includes the Amazon river and transports large volumes of water to the Atlantic Ocean. It has an area of about 7 million km^2.

Communities. A group of individuals that belong to different species and share an environment and exist together at a given place and time.

Decomposition. A continuous natural process which starts immediately after death and causes the organic substances of a body to break down into much simpler forms of matter.

Ecosystems. The complex of living organisms, their physical environment, and all their interrelationships in a particular unit of space and time. An ecosystem can be categorized into both abiotic and biotic constituents which together involve two major forces: flow of energy and cycling of nutrients.

Flooding. Land surface covered with water table, caused by association of rainyfall, landform, and poorly drained soils.

Flood pulse. Pulsing of river discharge causing predictable or unpredictable flooding of lateral river floodplains and functioning as the main driving force behind the productivity and interactions of the main biota in river plain systems.

Hydrology. The science that encompasses the study of water on Earth, as well as the source and movement of water, its physical and chemical properties, and finally how it interacts with living components.

Meander. Or oxbow lake. The remains of the bends of a winding river in an incipient slope and that was abandoned by the flowing waters. They correspond to lakes of still or stagnant waters.

Productivity. The rate of production of new biomass by an individual, population, or community; the fertility or capacity of a given habitat or area.

Seasonal. Relating to or characteristic of a particular season of the year (e.g. dry, wet). It can fluctuate or restricted according to the season or time of year.

Terrestrial ecosystems. A land-based community of organisms and the interactions of biotic and abiotic components in a given area. Examples of *terrestrial ecosystems* include the tundra, taigas, temperate deciduous forests, tropical rainforests, grasslands, and deserts.

Vegetation types. Describe the general characteristics of the vegetation cover of an area, where life forms are represented according to site and time (such as grass, shrub, submerged aquatic) that gives its character to a plant community.

Wetland. Areas where water covers the soil or is present either at or near the surface of the soil all year or for varying periods of time during the year, including during the growing season.