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Key Points:

- Tropical forests' biodiversity promotes diverse ecosystem services (ESs), but relationships between biodiversity and ESs are not obvious
- Different ES types are related to different attributes of biodiversity: structure, composition, and functions
- Savannization of Amazonia could impact the types of ESs provided by rain forests, particularly climate regulating services

Correspondence to:
L. S. Borma,
laura.borma@inpe.br

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Author Contributions:
Conceptualization: L. S. Borma, M. H. Costa, H. R. da Rocha, J. Arieira, N. C. C. Nascimento, G. Ambrosio, C. A. Nobre
Formal analysis: L. S. Borma, M. H. Costa, H. R. da Rocha, J. Arieira, N. C. C. Nascimento, C. Jaramillo-Giraldo, G. Ambrosio, R. G. Carneiro
Funding acquisition: C. A. Nobre
Investigation: L. S. Borma, M. H. Costa, H. R. da Rocha, J. Arieira, N. C. C. Nascimento, C. Jaramillo-Giraldo, G. Ambrosio, R. G. Carneiro, M. Venzon, A. F. Neto, B. F. A. Oliveira, R. Rajão
Project Administration: C. A. Nobre
Resources: C. A. Nobre
Supervision: L. S. Borma, M. H. Costa, C. A. Nobre

Beyond Carbon: The Contributions of South American Tropical Humid and Subhumid Forests to Ecosystem Services

L. S. Borma[1], M. H. Costa[2], H. R. da Rocha[3], J. Arieira[4], N. C. C. Nascimento[4], C. Jaramillo-Giraldo[2,4], G. Ambrosio[2,5], R. G. Carneiro[1], M. Venzon[6], A. F. Neto[4], R. van der Hoff[7], B. F. A. Oliveira[8], R. Rajão[7], and C. A. Nobre[4]

[1]Divisão de Impactos, Adaptação e Vulnerabilidade (DIIAV), Instituto Nacional de Pesquisas Espaciais – INPE, São José dos Campos, Brazil, [2]Departamento de Engenharia Agrícola, Universidade Federal de Viçosa – UFV, Viçosa, Brazil, [3]Instituto de Astronomia, Geofísica e Ciências Atmosféricas/Universidade de São Paulo – IAG/USP, São Paulo, Brazil, [4]Instituto de Estudos Climáticos, Universidade Federal do Espírito Santo – UFES, Vitoria, Brazil, [5]Copernicus Institute of Sustainable Development, Utrecht University, Utrecht, The Netherlands, [6]Agriculture and Livestock Research of Minas Gerais – EPAMIG, Minas Gerais, Brazil, [7]Laboratório de Gestão de Serviços Ambientais (LAGESA), Universidade Federal de Minas Gerais, UFMG, Belo Horizonte, Brazil, [8]Escritório Regional da FioCruz no Piauí, Teresina, Brazil

Abstract Tropical forests are recognized for their role in providing diverse ecosystem services (ESs), with carbon uptake the best recognized. The capacity of tropical forests to provide ESs is strongly linked to their enormous biodiversity. However, causal relationships between biodiversity and ESs are poorly understood. This may be because biodiversity is often translated into species richness. Here, we argue that focusing on multiple attributes of biodiversity—structure, composition, and function—will make relationships between biodiversity and ESs clearer. In this review, we discuss the ecological processes behind ESs from tropical humid and subhumid forests of South America. Our main goal is to understand the links between the ESs and those three biodiversity attributes. While supporting and regulating services relate more closely to forest structure and function, provisioning services relate more closely to forest composition and function, and cultural services are more related to structure and composition attributes. In this sense, ESs from subhumid forests (savannas) differ from those provided by the Amazon Forest, although both ecosystems are recognized as harboring tremendous biodiversity. Given this, if anthropogenic drivers of change promote a shift in the Amazon Forest toward savanna—the savannization hypothesis—the types of services provided will change, especially climate regulating services. This review emphasizes the importance of deeply understanding ecosystem structure, composition, and function to better understand the services ecosystems provide. Understanding that anthropogenic impacts on biodiversity occur through these three main attributes, it becomes easier to anticipate how humans will impact ESs.

1. Introduction

Tropical forests are key habitats for diverse organisms, and because of their wide global distribution, rich biodiversity, and long history of human use, they are also essential for providing a wide range of ecosystem services (ESs; Brandon, 2015; Brockerhoff et al., 2017; Gibson et al., 2011; Mori et al., 2017). Considerable attention has been devoted to tropical forests and their role as a natural climate solution for mitigating climate change. It is estimated that about 30% of all CO_2 emitted by human activities is removed from the atmosphere by these forests (Le Quéré et al., 2018). The important role of tropical forests as a carbon sink and stock has historically guided conservation pacts, programs, and policies for establishing targets associated with carbon storage and climate change mitigation. This role was important in developing several articles of the 1997 Kyoto Protocol (Swingland et al., 2002) and explicit policies for reducing emissions from deforestation and forest degradation through the REDD+ agreement (Pistorius, 2012). Several countries also set ambitious goals for restoring forests to reduce emissions or sequester carbon in the United Nations Framework Convention on Climate Change 2015 Paris Agreement. The land use, land cover change, and forestry (LULCCF) sector is included in many countries' first nationally determined contributions (NDCs) but with differing levels of specificity. Assuming full implementation of NDCs, Grassi et al. (2017) show that land use—and forests, in particular—emerges as a key component of the Paris Agreement: global land use will turn from a net anthropogenic source during 1990–2010 (1.3 ± 1.1 Gt CO_2e yr^{-1}) to a net sink of carbon by 2030 (up to -1.1 ± 0.5 Gt CO_2e yr^{-1}) and would provide a quarter of countries' planned emission reductions. Two tropical countries stand out regarding the magnitude of the LULCCF contribution: Brazil set ambitious goals of reducing greenhouse gas emissions by 43% by 2030 with

Writing – original draft: L. S. Borma, M. H. Costa, H. R. da Rocha, N. C. C. Nascimento, C. Jaramillo-Giraldo, G. Ambrosio, R. G. Carneiro, M. Venzon, A. F. Neto, B. F. A. Oliveira, R. Rajão

respect to the 2005 baseline, including restoration of 12 million hectares of forests, and committed to achieving zero net deforestation by 2030. And Indonesia has committed to a 41% decrease in emissions relative to a 2030 business-as-usual scenario. However, to some extent, the success of such policies may depend on a substantial increase in carbon prices to pay for carbon sequestration and storage (Koh et al., 2021).

Yet, these policies do not consider other benefits provided by forests; they underestimate the total value of ESs from tropical forests, that is, the benefits people obtain from standing tropical forest ecosystems. South American tropical forests are a source of diverse ESs for various groups of people. Among the multiple reasons to preserve these forests, climate-related motivations have become the most prevalent issue for scientific research and global environmental governance in recent years and have driven actions to maintain or increase forest carbon stocks (Dauvergne & Clapp, 2016). Such an approach may be useful to reduce greenhouse gases in the atmosphere (Chazdon et al., 2016) but may miss in considering various other ESs provided by tropical forests that are critical for human well-being. Beyond the carbon sink and storage services (biogeochemical processes of climate regulation), tropical forests also provide climate regulating ESs through biogeophysical processes. For example, tropical forests are responsible for an atmospheric cooling effect due to high evapotranspiration (ET) levels. Surface winds transmit this effect well beyond the boundaries of the forests (Coe et al., 2017). In addition to these climate regulating services, tropical forests also efficiently recycle water by means of several plant traits, such as deep rooting systems, high leaf area, and surface roughness that facilitates upward water vapor transport. These conditions, strongly related to the forest structure, increase rainfall over tropical forests compared to grass in grazing lands or soy crops (M. H. Costa et al., 2007). Other ES examples include protecting biodiversity, supporting water security (Costanza et al., 1997), and increasing agricultural resilience to climate change (M. H. Costa et al., 2019).

The multiple benefits furnished by keeping natural forests standing are not perceived clearly by many people (TEEB, 2010), which may encourage unsustainable management practices by different groups and threaten the long-term maintenance of forest-provided ESs (Alarcon et al., 2016). There is a need for communication from scientists about how tropical forests provide benefits other than carbon sequestration. In this context, science-based evidence should support policy design by highlighting the importance of the tropical forest's biodiversity, its benefits, and the socioeconomic risks of losing tropical forest ESs.

While it is widely recognized that having high biodiversity promotes a large suite of ESs, the relationship between biodiversity and ESs is not always straightforward (Brockerhoff et al., 2017; Mori et al., 2017). Biodiversity has been related to the provision of services such as pollination, soil fertilization, nutrient cycling, biomass production, and disease control (Thompson et al., 2012). On the other hand, services such as climate regulation (through biogeochemical or biogeophysical processes), natural disaster regulation, and water regulation have been described as being only weakly related or unrelated to biodiversity (MEA, 2005). It is important to note that, in these examples, the concept of biodiversity has been translated to species richness. This is probably a consequence of the prevalence of poor definitions of biodiversity, which do not make clear that biodiversity includes not only species richness, but also the ecological processes that produce and maintain the composition, structure, and functions of a given ecosystem (Franklin et al., 1981; Lamont, 1995; Noss, 1990).

Here, we argue that an analysis of the role of biodiversity in delivering ESs needs to recognize the three major components of biodiversity: composition, structure, and function (Franklin et al., 1981; Lamont, 1995; Noss, 1990). So, when we say that tropical forest ESs are closely related to biodiversity, we are saying that ESs are related to local forest composition (species and communities), structure (forest physiognomy), and function (i.e., processes through which species and environment interact via energy and matter transfers, and flow of populations through time). In this sense, all the ESs are related to the biodiversity through one or more of these attributes. In this context, it is easy to understand that increasing tree-species richness in a given stand will not necessarily increase all the ESs. For this to happen, it is necessary that the species interact in complementary ways in terms of how they maintain their functions through energy, water, and nutrient cycling inside the ecosystem (Forrester & Bauhus, 2016).

The relationship between biodiversity and ESs is an area of active research and is the focus of concentrated efforts of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBESs) and the International Union of Forest Research Organizations, among others (Brockerhoff et al., 2017; IPBES, 2019a). Understanding these issues is urgent given the speed with which we are losing global biodiversity (Dobson et al., 2006), a trend that is quite pronounced for the humid tropical forests of South America, South and Southeast

Asia, and Africa (Keenan et al., 2015). Because of this, in addition to focusing on the role of the biodiversity attributes—structure, composition, and function—in determining the ESs provided by tropical forests, we also highlight a paramount function of biodiversity, which is its ability to provide stability to the ecosystem, thus preventing abrupt changes from one equilibrium state to another in response to external or internal drivers of change (C. W. Runyan & D'Odorico, 2014).

This review focuses on tropical humid and subhumid forests in South America, encompassing the Amazon Forest, the Atlantic Forest, and South American tropical savannas. Our main goal is to present the ecological (i.e., physical, chemical, and biological) processes and functions underlying how tropical forests provide ESs, including their influence on climate patterns, fresh water, mitigation of natural disasters, biodiversity and habitat maintenance, food production, and human health. Rather than focusing on species richness (i.e., number or diversity of species), our focus is on three attributes—structure, composition, and functioning—of tropical forests. A secondary goal is to increase awareness of the noncarbon roles of tropical forests, which may help decision makers in developing and justifying sustainable land use policies for tropical forests. A third goal is to show how human actions that compromise the structure, composition, and function of tropical forests may influence ecosystem processes enough to change an ecosystem from an equilibrium state to a secondary equilibrium state. We also investigate how changes in structure and composition may compromise ESs provided by tropical forests. For example, we look at the Amazonian savannization hypothesis (Nobre et al., 1991) and discuss how local and global anthropic drivers such as deforestation and climate change may affect Amazon forest structure and composition, compromising the ESs this forest provides. Finally, we also highlight the important role of biodiversity (in terms of the three main attributes) in supporting the Amazon Forest's resilience in response to an abrupt change in the equilibrium state.

With these goals in mind, we have organized this review as follows: Section 2 presents the global distribution of the tropical forests and the importance of South American tropical forests in terms of the size of contiguous forests and species richness. We also present a brief geological history of these forests, how they are formed, and the human pressures they have been suffering. In Section 3, we present definitions of ecological process, ecosystem function, and ESs. In Sections 4–7, we present evidence of the tropical humid and subhumid forest ESs, with emphasis on the ecological processes and ecosystem functions behind these services. We use the same classification system used by the Brazilian Policy and Federal Payment Program for Environmental Services (Law 14.119 of 13 January 2021, hereafter, the Brazilian ESs Law) to differentiate between regulating, provisioning, cultural, and supporting services. In Section 8, we discuss the relation between biodiversity and the ESs and the role of the biodiversity attributes—composition, structure, and function—in generating the ESs. We also present the theory behind abrupt regime shifts in vegetated ecosystems. In Section 9, we present the status and trends of land cover changes in South American tropical forests. In Section 10, we review the possibility of a regime shift in the Amazon Forest toward a savanna-like vegetation type and the potential impacts of an eventual abrupt regime shift on the ESs provided by the Amazon Forest. In Section 11, we discuss how some concepts related to functioning of South America's humid and subhumid tropical forests apply to other tropical and subtropical forests in Africa and Southeast Asia. Finally, in Section 12, we conclude by discussing the importance of tropical forests in providing a suite of ESs and the consequences that forest loss and equilibrium state change may have on these ESs.

2. South American Tropical Forests

Tropical forests are characterized by the dominance of tree life forms that create a closed canopy and structurally complex arrangements (Banin et al., 2015). These forests grow in warm climates (annual mean temperature between 20°C and 30°C) with high levels of precipitation (usually >1,000 mm yr^{-1}) (Whittaker, 1975). They are typically associated with wet equatorial (Af), tropical monsoon (Am), and tropical wet-dry climate zones (Aw) (Zhao et al., 2005). The humid tropical climates (Af and Am) are subject to annual rainfall rates >1,500 mm yr^{-1} well distributed throughout the year and warm temperatures throughout the year (~25°C). The subhumid climate (Aw) also has high annual rainfall rates (>1,000 mm yr^{-1}) but has a longer dry season, reaching 5–6 months. In both humid and subhumid tropical climate conditions, the annual mean difference between precipitation (P) and potential evapotranspiration (ETP) is positive (P – ETP >0), implying a positive water balance that recharges groundwater and produces large, high-flow rivers. In the tropics, the rainfall amount and the durations of the dry and wet seasons are significant in determining the tropical forest types. Therefore, the tropical forest's structure, composition, and functioning can vary substantially according to climate patterns.

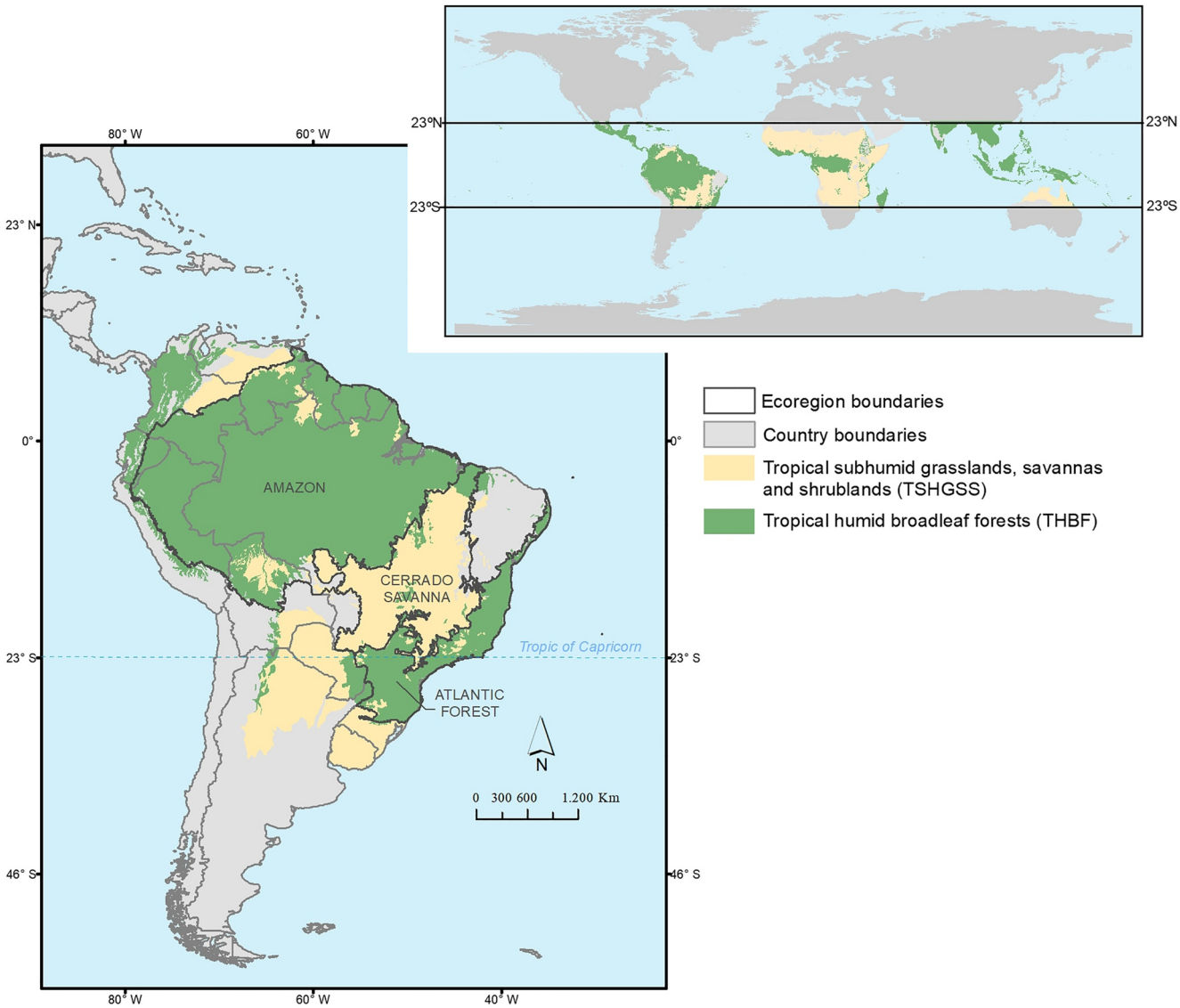

Figure 1. Distribution of tropical forests in South America and globally. Database from Olson et al. (2001).

In this review, we use the division of biomes proposed by Olson et al. (2001) (Figure 1), focusing on the South American tropical humid and subhumid forests and woody savannas. According to Olson et al. (2001), the global land cover is divided into 8 realms, 14 biomes, and 867 ecoregions. The ecoregions represent biotas, nested within the biomes and realms, containing distinct natural communities and species assemblages. Tropical humid forests correspond to the tropical humid broadleaf forest (THBF) biome from Olson et al. (2001). Globally, the THBF occupies 19.8×10^6 km^2 (13.4%) of the global ice-free land surfaces (GIFLSs); of this, 8.25×10^6 km^2 comprises Amazonian and Atlantic rain forests, which, together, occupy 45.1% of the South American continent (Table 1). Tropical savannas encompass the biome of tropical [subhumid] grasslands, savannas, and shrublands (TSHGSS) from Olson et al. (2001). Globally, TSHGSS occupies 20.2×10^6 km^2, or 13.7% of the GIFLS (Table 1). Together, the THBF and TSHGSS make up 66.8% of South America, 77.5% of the tropics, and 27.1% of the GIFLS (Table 1). Despite comprising less than 30% of the GIFLS, these forests are responsible for a large number and variety of ESs that benefit global, regional, and local populations. Below, we describe these forests in detail and how their ecosystem structure, composition, and functions ultimately generate ESs.

There are three major categories of South American THBF and TSHGSS: the Amazon forest (the dominant vegetation type of the Amazon Forest biome), the Atlantic Forest (the dominant vegetation type in the Atlantic

Table 1
Areas Covered by THBF and TSHGSS in South America and Globally

Biome	Area in SA[a] (10^6 km^2)	Percentage of SA	Global area (10^6 km^2)	Percentage of GIFLS[b]	Tropical area (10^6 km^2)	Percentage of tropics
THBF[c]	8.25	45.1	19.78	13.4	280.55	40.4
Amazon Forest	6.91 (86%)	37.8				
Atlantic Forest	1.34 (11%–26%)	7.3				
TSHGSS[d]	3.97	21.7	20.18	13.7	257.44	37.1
Brazilian Cerrado	1.91 (54%)	10.94				
Other TSHGSS[e]	2.06	11.3				

Note. Together, these two types of forests account for 66.8% of the South American continent, 27.1% of the global ice-free land surface (GIFLS), and 77.5% of global tropical areas. Data from Olson et al. (2001). The numbers in parenthesis refer to the percentage of forests still remaining in the biomes.

[a]SA area of 18.13 × 10^6 km^2. [b]GIFLS area of 147.34 × 10^6 km^2. [c]THBF—tropical humid broadleaf forest. [d]TSHGSS—tropical subhumid grasslands, savannas, and shrublands. [e]Other SA TSHGSS: Chaco, Beni savanna, Guyanan savanna, Venezuelan Llanos, montane savanna, Uruguayan savanna.

Forest biome), and the tropical savannas (the dominant vegetation type of the South American tropical savannas, of which the larger regions are the Brazilian Cerrado and the Venezuelan Chaco) (Figure 1). The largest, most contiguous, and best-known tropical humid forest is the Amazon Forest, which spans about 6.9 × 10^6 km^2, occupying parts of Colombia, French Guiana, Suriname, Guyana, Venezuela, Ecuador, Peru, Bolivia, Paraguay, and Brazil. Brazil contains approximately 3.1 × 10^6 km^2 of the Amazon's area, mainly composed of intact forests (Tejada et al., 2019).

The Amazon forest is the humid forest mainly found in the Amazon river basin. The Amazon river basin covers 6.3 × 10^6 km^2 and is the largest watershed on Earth, through which flows about 15%–20% of global fresh water (Giffard et al., 2019). Stretching across the midwestern portion of South America, the Amazon basin is bounded to the south by the Brazilian plateau (~700 to 1,100 m in height), to the west by the Andean shield (~5,000 m), to the north by the Guyana shield (~1,000 m), and to the northeast by the Atlantic Ocean. The Andean shield is a barrier for the easterly winds that turn southward and favor regional precipitation, water recycling, and air moisture transport downwind (Section 4.1). The Amazon basin experiences a wide range of rainfall (1,700–3,000 mm yr^{-1}), with no dry season in the northwest and a dry season increasing in length from one to four months as one moves southward and eastward across the basin (Sombroek, 2001). Rainfall reaches 300 mm mo^{-1} in the wet period and less than 100 mm mo^{-1} during the dry period (Marengo, 2004; Sombroek, 2001).

Although composed of a mosaic of many specialized ecosystems, including (e.g.,) savanna, mangrove, and *buritizal* (a type of palm swamp; plural: *buritizais*), the Amazon forest is broadly classified into two major categories: upland forests (i.e., nonflooded forests) and seasonally flooded forests. The upland forests include dense, open, dry, and montane forests that vary in biomass, canopy height, species dominance, and leaf phenology (J. Pires & Prance, 1985). Seasonally flooded forests include lowland forests subject to seasonal flooding, covering extensive areas along the lower streams of all major Amazon rivers (Junk et al., 2010). The Amazon's seasonally flooded forests are locally classified into *várzea* and *igapó*. The várzeas occur along the white-water rivers, such as the Solimões-Amazon River, and are rich in nutrients from the eroded sediments from the Andean and sub-Andean shields. The igapós occur at the margins of the clear but black-water rivers. These rivers flow through more ancient geologic regions, such as the Guiana shields, and therefore transport low levels of sediments and nutrients. The Amazon floodplain occupies about 17% of the entire Amazon basin, and it is more than 70% covered by seasonally flooded forests (Hess et al., 2015; Melack & Hess, 2010).

In the Amazon River basin, the transport of floodwater from the river to the floodplain plays a vital role in ecological processes. Seasonal flooding (aquatic phase) feeds the várzeas with nutrient-rich waters. Depending on the region and its geomorphology, the river water level can vary by as much as 10–15 m for approximately 4–5 months each year (Junk & Wantzen, 2004). When the water level drops (terrestrial phase), it gives rise to a mosaic of diverse and interconnected patches of forests, meadows, and water bodies that configure a habitat for diverse terrestrial and aquatic biota (Junk, 1984; Junk et al., 2010). The várzeas are among the most biologically productive environments in the Amazon (Alsdorf et al., 2010; Junk et al., 2007).

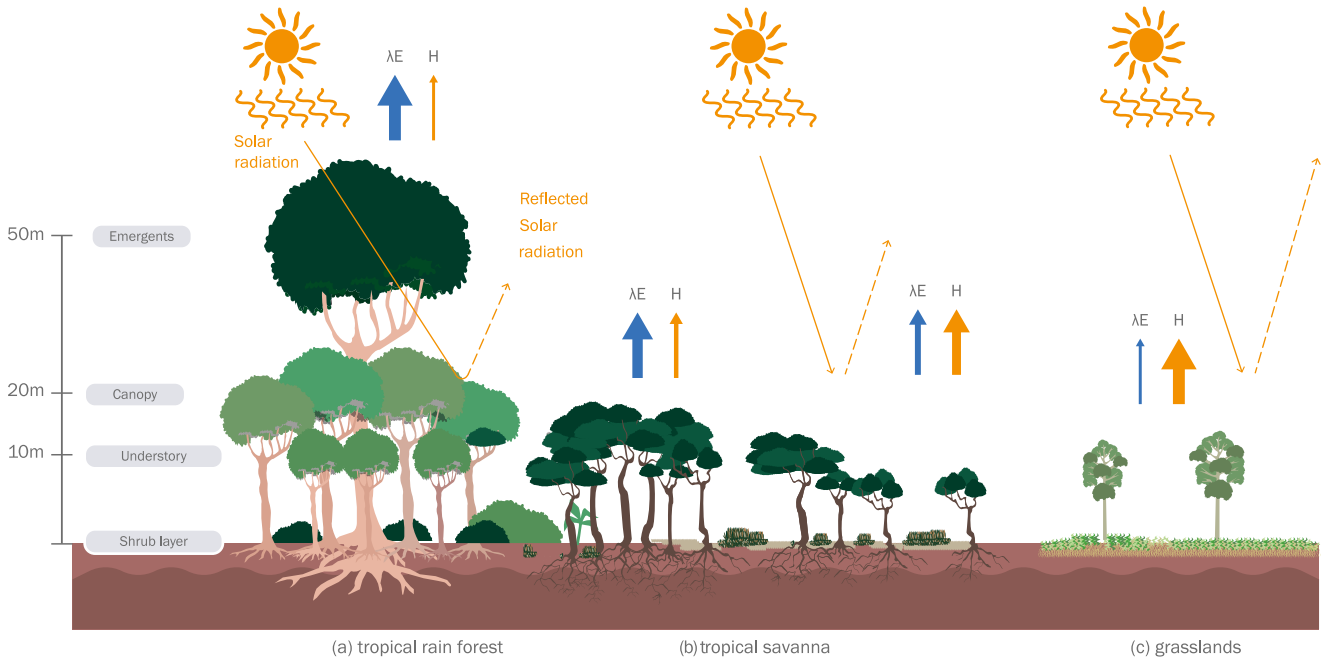

Figure 2. Structure and composition of (a) tropical rain forest, (b) tropical savanna (Brazilian Cerrado and its diverse physiognomies), and (c) grasslands. Blue arrows mean latent heat flux (λE), and orange arrows mean sensible heat flux (H).

The dynamic nature and heterogeneous structure of the várzea supports an assortment of ESs, including fertile soils for agriculture, flood mitigation, water cleansing, and abundant natural resources such as fishes, timber, fruits, medicines, and wildlife. This is why the várzea forest is also known as "working forest," where human residents have developed productive land-use systems integrated into the environment (Pinedo-Vasquez et al., 2011).

The Atlantic Forest is another humid (or rain) forest of South America. It is the second-largest tropical rain forest in South America. Its unique geomorphological complexity, edaphic heterogeneity, and thermal gradients contribute to a wide range of forest types and species endemism (Cantidio & Souza, 2019; Correia et al., 2020; Oliveira-Filho & Fontes, 2000; Ostroski et al., 2020). The Atlantic Forest mosaic includes ombrophilous, semi-deciduous, deciduous, and pioneer forest formations (e.g., mangrove), which are classified based on the altitudinal gradient in montane, submontane, and lowland forests. These formations are distributed according to the duration of the dry season, the distance from the ocean, and altitude. This forest originally stretched for 1.36×10^6 km^2 along the east coast of Brazil, extending into northeastern Argentina and southeastern Paraguay through a plateau in the central and southeastern interior (Cantidio & Souza, 2019; Morellato & Haddad, 2000). Today, 11%–26% of its original cover remains, generally occupying small fragments (<50 ha) surrounded by agricultural and urban areas (M. C. Ribeiro et al., 2009, 2011).

Montane tropical cloud forests (MCFs) comprise the montane forests that are frequently exposed to clouds at the canopy level. They are found near shoreline plateaus and crests of mountain ranges in the Atlantic Forest biome and can be considered natural water reservoirs (Bruijnzeel, Kappelle, et al., 2011). That is because of their capacity to produce rainfall due to the continuous condensation of vapor on the leaves. Besides their role in climate regulation, several hotspots include MCFs because these forests are considered areas of high endemism (Aldrich et al., 1997; N. Myers et al., 2000).

Tropical Savannas are the second-largest biome in South America (Olson et al., 2001), covering about 4×10^6 km^2 or ~22% of South America (Table 1). In this subhumid forest, the savanna vegetation type is distributed among some larger contiguous areas and many smaller disjointed patches in Brazil, Bolivia, Venezuela, Colombia, and Guyana's coastal regions (Pennington et al., 2019) (Figure 2). South American tropical savannas include the Beni savannas in Bolivia, Llanos savannas in Venezuela and Colombia, dry and humid Chaco in Paraguay, and the Cerrado in Brazil, Bolivia, and Paraguay. The Cerrado occupies the largest extent of South America's tropical subhumid forests, covering approximately 1.9×10^6 km^2, mostly located in Brazil (Table 1). The

Venezuelan-Colombian Llanos is the second-largest savanna-dominated region, covering more than 400,000 km^2 of western Venezuela and Colombia (Borghetti et al., 2019). Both have high habitat complexity, endemism, and plant species exchange compared to other tropical savannas (Dinerstein, 1995).

The Brazilian Cerrado biome shows different physiognomies—often differentiated based on the tree height and the density of trees and grasses—that are spatially distributed mostly according to the precipitation seasonality, soil fertility and drainage capacity, and fire occurrence (Furley & Ratter, 1988). The climate has a 4- to 5-month dry season between May and September, with large spatial variability of annual rainfall between 800 and 2,000 mm and temperatures between 18°C and 28°C (Oliveira-Filho & Ratter, 2002). Soils are generally deep and permeable, with low fertility (Buol, 2009). The physiognomies of the Brazilian Cerrado (in % of areal fraction) are the *cerradão* (11%), with taller trees and great vegetation density, found usually on upland soils; the *cerrado sensu stricto* (70%), with shorter trees and shrubs and generally found on dystrophic, low-pH soils (Lopes & Cox, 1977); and the *campo cerrado* (18%), with areas of grass and scattered shrubs/small trees, *campo sujo* (grass and sparse shrubs), and *campo limpo* (grass). Light and water availability are the main abiotic drivers regulating the length of the growing season, the timing of leaf production, and the phenological synchrony among cerrado species (Alberton et al., 2019). The flora exhibits morphological and physiological adaptations to climate and edaphic limitations. Traits that help the forest to survive during the dry season include tree leaf senescence and litterfall, strong stomatal control, increase of water withdrawn from internal stem storage and uptake by deep roots (Buol, 2009; J. M. C. Da Silva & Bates, 2002), and dormancy of grasses. Beyond being an important carbon stock, deep roots help to channel the rainfall back into deep soil reservoirs as a mechanism for aquifer recharge (Klink et al., 2020; Lahsen et al., 2016).

2.1. Geologic Evolution of South American Tropical Forests

Throughout geological times, the distribution of these three South American forest and savanna biomes were determined by patterns of climate, soils, and possibly atmospheric CO_2 concentrations. Over the eons, their distribution and biodiversity have been shaped by large-scale geophysical characteristics. Neotropical rain forest plants reached an apogee of diversity during the Eocene (ca. 56–34 million years ago, Ma) when high greenhouse gas concentrations and hot (13°C–15°C above pre-industrial levels), wet climates predominated (Jaramillo et al., 2010). Drier seasons and cooler temperatures of the early Oligocene (ca. 30 Ma) divided South American rain forests into the Amazon and Atlantic rain forests, establishing the Dry Diagonal subhumid forests between them (L. P. Costa, 2003; Sobral-Souza et al., 2015; Thode et al., 2019). These vegetational changes coincided with the uplift of the Mantiqueira Mountains of eastern Brazil and of the northern Andes, which began 20 Ma. As the mountains reached heights of 2.5 km or more, the air had to rise over them, causing high rainfall rates and fundamentally changing the climatic regime over South America.

The mountain uplift contributed to substantial changes in South American air circulation. Increasingly drier climates led to the expansion of open savanna vegetation types and were accompanied by substantial changes in species composition (e.g., palms), the origin of C4 grasses (Bouchenak-Khelladi et al., 2014; Vicentini et al., 2008), and the expansion of grasslands and open woodlands at the expense of closed-canopy forested habitats (Edwards et al., 2010).

Temperature estimates for cool glacial periods, such as the Last Glacial Maximum ca. 21,000 years ago, vary between 1°C and 9°C cooler than the present. These cooler temperatures caused advances of high glaciers in the central Andes. In addition, the South American monsoon system was weaker, the trade winds were more zonal, and precipitation rates in the Amazon were lower; these conditions, along with lower CO_2 concentrations during glacial periods, coincided with the shrinkage of the rain forests to small refugia (Arruda et al., 2018; Haffer, 1969; Levis et al., 1999; Mayle et al., 2000).

Today and throughout prehistory, environmental complexity associated with edaphic, topographic, and climate variability has been responsible for the presence of transitional vegetation bordering some biomes and ecoregions and explains enclaves of habitats in ecoregions that differ from their assigned biome (Olson et al., 2001; Pennington et al., 2018). The forest-savanna boundary in the southeastern Amazon exemplifies this transition; it is governed by a delicate climate balance, knowledge of which is critical to understanding community patterns and biome distribution changes (Furley & Ratter, 1988). Brazilian Cerrado enclaves are also found within tropical humid forest biomes (the Amazon and Atlantic Forests).

Table 2
Estimated Number of Species, Area Covered (10^6 km^2), and Percentage of Remaining Vegetation in Amazon Forest (AM), Atlantic Forest (AF), and Brazilian Cerrado (BC)

Biodiversity	Amazon Forest	Atlantic Forest	Brazilian Cerrado
Vascular plants	15,000–55,000	20,000[a]	12,356
Trees	16,000	7,000[a]	1,870
Mammals	425 (399[a])	497 (321[a])	251
Reptiles	371	312 (200[a])	180
Amphibians	427	625 (280[a])	113
Birds	1,300	861 (620[a])	837
Area covered (km^2)	6.9×10^6	1.3×10^6	1.9×10^6
Vegetation remaining (%)	86	11–26	54

Sources. R. Moraes et al. (2021) (AM), N. Myers et al. (2000) (AF), R. C. Mendonça et al. (2008) (BC), Zwiener et al. (2021) (AF), Paglia et al. (2012) (AM-Brazil), Bogoni et al. (2017), Protázio et al. (2021), Graipel et al. (2017), and Brasil (2007).
[a]Occurrence in Brazil.

2.2. Biodiversity of South American Tropical Forests

The world's most biodiverse regions include the western Amazon, Brazil's Atlantic Coast, and Mesoamerica (Dirzo & Raven, 2003). Common characteristics of these ecoregions include evergreen and semievergreen (semideciduous) forests, high endemism, high spatial distribution of species (beta diversity), and high species richness. Compared to tropical Africa (30,000–56,000 spp.), the Neotropics holds up three times more seed plants (90,000–118,000) (Antonelli & Sanmartín, 2011; Raven et al., 2020). High structural complexity of intact forests is attributed to annual precipitation and seasonality, and to water balance and storage (Ehbrecht et al., 2021). Their uniqueness distinguishes them in terms of their taxonomy, geomorphological characteristics, disturbance regime, and evolutionary history (Dinerstein, 1995; J. F. Silva, 1996; Silva de Miranda et al., 2018).

The Amazon lowland harbors more than 10% of all the vertebrate fauna and vascular plant diversity in the world (Mittermeier et al., 2003) and has an estimated 15,000–55,000 vascular plant species, including 16,000 tree species (Table 2), which represents about 25%–30% of global tree diversity (Dirzo & Raven, 2003; Ter Steege et al., 2013). The region has 14,003 seed plant species already cataloged, of which 6,727 are tree species (D. Cardoso et al., 2017; Fine et al., 2004; Ter Steege et al., 2015). In addition, the region is home to approximately 425 species of mammals—which constitutes one-third of South America's 1,260 mammal species (Bonvicino & Weksler, 2012)—1,300 birds, 427 amphibians, and around 2,406 species of fish (Table 2) (J. M. C. da Silva et al., 2005; Junk et al., 2007; Zapata-Ríos et al., 2021). In the northwest and central Amazon, 1 ha may hold more than 300 different species of plants (Amaral et al., 2000; Gentry, 1988).

In the Atlantic Forest, highly heterogeneous landscapes and the geologic history of climate oscillations (Carnaval & Moritz, 2008) have resulted in an extremely biodiverse area harboring 1%–8% of total world biodiversity (J. M. C. Silva & Casteleti, 2003). The Atlantic Forest consists of the second main source of Neotropical diversity (Antonelli et al., 2018). The biome supports around 20,000 vascular plants (Table 2), including 8,000 endemics (2.7% of the global total), and 1,361 vertebrates, 567 of which are endemics (2.1% of the global) (N. Myers et al., 2000). It has half (50.5%) of the Brazilian fauna species threatened with extinction (ICMBio/MMA, 2018). Thus, the Atlantic Forest biome is recognized as a biodiversity hotspot, harboring ~35% of Brazilian biodiversity, with notably high endemism and species richness (Taffarello et al., 2017).

The Brazilian Cerrado is the richest savanna in the world (Simon & Pennington, 2012) in terms of species, with an estimated 160,000 species of plants, animals, and fungi (B. F. S. Dias, 1992). R. C. Mendonça et al. (2008) counted 12,356 vascular plants. The lowland grassland and forests of the Venezuelan Llanos hold a much lower diversity, with 3,200 vascular plants (De Stefano et al., 2009). Although the savanna physiognomy is characterized mostly by the presence of scattered trees and shrubs, savannas have a great richness of tree species, often associated with patches of dry forests, gallery forests, savanna forests (cerradão), and palm swamps (Borghetti et al., 2019; Françoso et al., 2016). From the 6,024 species of plants counted for the Brazilian Cerrado, 2,870 are found in forests, 802 in typical savanna physiognomies, and 672 in grasslands (J. F. F. Ribeiro & Walter, 1998). Insects are among the richest groups of species present, numbering ~90,000 species (B. F. S. Dias, 1992). A floristic survey revealed that of 951 species identified in Brazilian Cerrado locations (representing a small fraction of the Brazilian Cerrado's total plant diversity), ~35% were restricted to a single place and no species were found in all areas (Ratter et al., 2003). Recent estimates indicate that the Brazilian Cerrado is the refuge of 13% of butterflies, 35% of bees, and 23% of termites in the tropics (Fernandes, 2016).

2.3. Structure and Composition of South American Tropical Humid and Subhumid Forests

The favorable conditions for forest development in the tropics have resulted in a very tall Amazon Forest biome and a dense and evergreen canopy in many areas. In addition, the forests maintain their own existence throught several complexes and interplayed processes. Forest's structure influences the amount of solar radiation that reaches the forest floor (i.e., the light-related processes; Section 7.3). The vertical gradient in light distribution

means that the forest floor is dominated by species that are more shade tolerant. The low light incidence influences the development of the understory (or undercanopy) and gives rise to a very stratified canopy, made up of two or three levels (e.g., emergent, main canopy, and undercanopy) (Figure 2). At the forest floor, there is a large amount of litterfall, mosses, and lichens. Light-condition gradients (e.g., from canopy gaps) influence plant chemical characteristics (e.g., concentrations of phenolic compounds and tannins). At the same time, however, gaps in the forest canopy produced locally by tree fall create a mosaic of plant communities of different ages and compositions (Schnitzer & Bongers, 2011). For instance, trees may adopt different photosynthetic responses (e.g., specific leaf area, maximum photosynthetic capacity) to the broad range of light environments in the Atlantic Forest, allowing them to develop under different degrees of canopy openness; and some trees may change photosynthesis mechanisms that deal with excessive light in response to spatiotemporal variation in water availability (Vitória et al., 2019). Savannas have a less dense vegetation structure when compared to rain forests, resulting in different arrangements of trees and grasses (Figure 2). Spatial patterns of tree height and density are determined chiefly by precipitation seasonality, fire frequency, soil fertility, and drainage (Furley & Ratter, 1988).

3. Ecosystem Services, Ecosystem Functions, and Ecosystem Processes

3.1. Ecosystem Services and Classification Systems

ESs encompass the benefits that ecosystem provide to human beings through their natural functioning (Costanza et al., 1997, 2017). The concept emerged in the 1980s (Ehrlich & Ehrlich, 1981; Ehrlich & Mooney, 1983) and became established in the late 1990s (Costanza et al., 1997; Daily, 1997; MEA, 2005). The Millennium Ecosystem Assessment (MEA), a comprehensive assessment requested by the United Nations Secretary-General, defines ESs simply as the benefits people obtain from ecosystems and classifies ESs into four primary categories (Table 3): (a) regulating services, which are the services that regulate and maintain ecosystem functioning, such as climate regulation, water regulation, natural disaster control and/or mitigation, and disease control; (b) provisioning services, which comprise the goods that people obtain from ecosystems, such as food, raw materials, and medicines; (c) cultural services, which includes nonmaterial benefits, such as social and spiritual identity, physical and mental health, recreation, educational and esthetic value, and ecotourism; and (d) supporting services, which comprise ecosystem functions that guarantee the provisioning of the other ESs (Costanza et al., 2017; MEA, 2005).

The valuation of ESs and ESs payment systems are the pillars of recent legislation passed in Brazil (Law 14.119 of 13 January 2021), which instituted the Brazilian Policy and Federal Payment Program for Environmental Services (Brazilian ESs Law). With this legislation, Brazil is attempting to advance in using and consolidating economic instruments for environmental protection. This legislation assumes the same categories as the MEA (2005), but with some small redefinitions (Table 3). For example, while Costanza et al. (2017) and MEA (2005) consider pollination, seed dispersal, pest and disease control, and decomposition of waste to be regulating services, the Brazilian ESs Law considers them supporting services, since humans do not directly assimilate their benefits. Moreover, the Brazilian ESs Law recognizes a broader range of cultural services by including any nonmaterial benefit as a cultural service. That is why we include the important roles of the forests to human health as cultural (or nonmaterial) services (Section 6.1).

The financial definition of the ESs has evoked criticism for focusing mainly on the economic benefits of natural ecosystems. This recognition led to more holistic approaches in ESs theory and application. One of these approaches is the concept of nature's contributions to people (NCPs; Díaz et al., 2015), which is used by the IPBES (IPBES, 2019a). This concept emphasizes nonmaterial benefits by more strongly stressing aspects such as learning and inspiration, physical and psychological experiences, supporting identities, and the capacity of ecosystems to keep options open to support good quality of life in the future (Díaz et al., 2018) (Table 3). The NCP concept recognizes that perception of the value of environmental benefits varies among different groups of people, with some groups placing greater importance on values beyond economic measurement. This concept also recognizes that drawing on diverse sources of knowledge is necessary for supporting human well-being (Díaz et al., 2015, 2018).

There exists a concern that valuing nature and its services will ultimately lead to its commodification and marketization. More specifically, this criticism suggests that nature, once its values are identified and expressed in monetary terms, will become a market commodity and, like any other commodity, subject to free trade. Though these are valid concerns, it could be argued that essential ESs are already being "traded" in precisely this manner,

Table 3
Classification Systems Used to Group Ecosystem Services (ESs) According to the Millennium Ecosystem Assessment (MEA, 2005), the Brazilian Policy and Federal Payment Program for Environmental Services (Brazilian ESs Law; Brasil, 2021), and the IPBES (International Panel of Brazilian Ecosystem Services)

Costanza et al. (1997, 2017)	MEA (2005)	Brazilian ESs Law (2021)	Díaz et al. (2018) and IPBES
Supporting and habitat services	Supporting services		Supporting and regulation services
Nutrient cycling; and refugia (nursery, migration habitat)	Biodiversity; nutrient cycling and photosynthesis, primary production; and soil formation	Maintenance of biodiversity and genetic heritage; nutrient cycling; soil formation; soil fertility maintenance or renovation; pollination and seed dispersal; and regulation of pests and human disease vectors	Habitat creation and maintenance; pollination and dispersal of seeds and other propagules; regulation of air quality; regulation of climate; regulation of ocean acidification; regulation of freshwater quantity, location, and timing; regulation of freshwater and coastal water quality; formation, protection, and decontamination of soils and sediments; regulation of hazards and extreme events; regulation of detrimental organisms and biological processes; and capacity of ecosystems and habitats to keep options open to support good quality of life
Regulating services			
Gas regulation; climate regulation; disturbance regulation (storm protection and flood control); erosion control and sediment retention; water regulation (e.g., natural irrigation and drought prevention); waste treatment; soil formation; pollination; and biological control	Air quality regulation; climate regulation; natural hazard regulation; erosion regulation; water regulation; water purification and waste treatment; pollination; and regulation of pests and human diseases	Air purification; carbon uptake; natural hazard regulation (storm protection, flood control, erosion control, and slope stabilization); and water cycle regulation	
Provisioning services			*Material goods*
Food production; water supply; raw materials; and genetic resources	Food; fresh water; fiber and ornamental resources; genetic resources; and biochemicals, natural medicines, and pharmaceuticals	Food; fresh water; and wood, fiber, extracts, etc.	Energy; food and feed; materials, companionship and labor; and medicinal, biochemical, and genetic resources
Cultural services		*Cultural services and nonmaterial goods*	*Nonmaterial goods*
Recreation; and cultural	Cultural diversity; spiritual and religious values; knowledge systems; educational values; inspiration; esthetic values; social relations; sense of place; cultural heritage values; and recreation and ecotourism	Recreation; tourism, cultural identity; spiritual and esthetic experiences; and intellectual development	Learning and inspiration; physical and psychological experiences; and supporting identities

Note. In this paper, we follow the Brazilian ESs Law (Brasil, 2021) classification.

sometimes for an implicit price of zero or just the cost of the land underneath the ecosystems. Thus, placing a value on nature's ESs should not be misinterpreted as "putting a price on nature." Rather, ESs valuation should be regarded as both a model for communicating to decision-makers in their economics-dominated language, and a toolkit for evaluating and integrating good stewardship into their decisions.

Because one of the goals of this manuscript is to raise awareness and increase visibility of the value of the tropical forests to support sustainable land use policies for tropical South America, we have opted to use the term "ESs" instead of "NCPs" throughout this review. However, our intention is not to dismiss the less tangible benefits that NCPs focus on but to include them within the overarching concept of ESs. Besides, despite the conceptual differences, the ES types listed among the NCPs do not differ much from the services listed in the IPBES and

the Brazilian ESs Law (Table 3). Therefore, in this paper, we choose to work with the classification of services according to the Brazilian ESs Law.

3.2. Ecosystem Functions and Ecological Processes

Following Costanza et al. (1997), ESs are defined as "*the ecological characteristics, functions or processes that directly or indirectly contribute to human wellbeing: that is, the benefits that people derive from functioning ecosystems*." According to this definition, ESs encompass not only ecological characteristics of a given ecosystem but also underlying ecological processes and functions. In the literature on the ESs, sometimes ecosystem functions and ecological processes are treated as being the same thing. However, differences do exist between processes and functions, and we argue that this understanding is an important step toward better considering ESs in the policies and practices of tropical forest conservation.

Ecosystems are defined as complexes where biotic and abiotic components interact through physical, chemical, and biological processes (*ecological processes*) in response to the availability of energy (radiation and heat) to cycle mass (water, nutrients, and carbon) (Odum, 2007). Since ecosystems are thermodynamically open, they exchange matter and energy with the environment (Currie, 2011; Odum, 2007). This means that the stability of an ecosystem can be affected by external agents, such as climate changes or selective logging. *Ecosystem functions* are the different responses of each ecosystem to the same drivers—energy, water, and nutrient flows or cycles—that comprise the *ecological processes*. For example, the partitioning between latent and sensible heat flux (ecological processes) is different if the solar radiation reaches a grassland or a humid forest; this results in different local climates and, consequently, in different rates of nutrient cycling (ecosystem function). Ecosystem functions maintain and support (i.e., drive) the integrity of ecosystems (i.e., their stability) and are of great importance because they support other services—regulating, provisioning, and cultural (Brockerhoff et al., 2017; Currie, 2011; Mace et al., 2012). That is why, in the field of ESs research, ecosystem functions are considered supporting services. Additionally, human actions that result in positive or negative impacts on ESs occur mainly through changes in the ecosystem functions (e.g., Brockerhoff et al., 2017). In Section 7, we describe the ecosystem functions (or supporting services), and in Section 8, we describe how these functions can be adversely affected by human actions.

According to Brockerhoff et al. (2017), ecological processes are organism centered, ecosystem functions are ecosystem centered, and ESs are human centered. The differentiation of such concepts is not only a semantic question. It is the basis to understand the natural science behind the ESs, how they are produced, how they interact, and how they can be adversely affected by human actions, through drivers such as land use and land cover changes and climate changes.

4. Tropical Forests and Regulating Services

According to the Brazilian ESs Law (Brasil, 2021), regulating services are "those that contribute to the maintenance of the stability of ecosystem processes, such as carbon sequestration, air purification, moderation of extreme weather events, maintaining the balance of the hydrological cycle, minimizing floods and droughts and controlling the critical processes of erosion and landslides." In this section, we present evidence of the regulating services provided by the tropical forests, with a focus on climate regulation (Section 4.1) and water cycle regulation (Section 4.2).

4.1. Climate Regulation

As a result of future climate forecasts and the effects that anthropogenic climate change is already having on the functioning of the Earth system—such as, for example, the increased frequency and severity of extreme climate events such as droughts and floods—increased attention is being paid to the role of humid and subhumid tropical forests in carbon sequestration and storage. In fact, tropical forests cycle 34% of the Earth's surface gross primary production (Beer et al., 2009) and represent about one half of the terrestrial carbon sink (Pan et al., 2011). However, through its structure, composition, and functions, tropical forest biodiversity is also responsible for several noncarbon ESs.

The interactions between vegetation and climate (particularly in terms of rainfall and temperature patterns) throughout the water cycle occur through biogeophysical and biogeochemical processes (see a review from

Spracklen et al. (2018)). Biogeophysical processes refer to water and heat flows between the land surface and atmosphere. Biogeochemical processes refer to the flows of trace gases (in particular CO_2) and aerosols (occurring as natural vegetal nanoparticles or by-products of forest burning) (see Spracklen et al., 2018). Tropical forest structure, with its different canopy layers and emergent trees, favors the land-surface and atmosphere fluxes. In a dense, covered, closed forest, the upper two thirds of the canopy is connected to the atmosphere (Seidler et al., 2013). Through photosynthesis, tropical forests absorb and store large amounts of carbon, which would otherwise be in the atmosphere as CO_2, increasing global temperatures and promoting changes in the global climate. That is why carbon uptake has been recognized as a vital climate regulation ES for tropical forests. However, carbon uptake is only one (albeit very important) way by which tropical forests exert control over the climate (Ellison et al., 2017; Keys et al., 2016, 2019). Below we present other important mechanisms by which tropical forests help to maintain the climate, such as thermal regulation, raifall recycling and moisture transport, and duration of the rainy season.

4.1.1. Thermal Regulation

The variability of the air temperature at the land surface is controlled primarily by the seasonality of incoming solar radiation, altitude (cooling with height), regional factors (the transient influence of air masses—maritime, polar, etc.), effects of complex terrain, and the land cover (Bonan, 2008). Under the control of large-scale drivers, the surface air temperature at the local scale is the ultimate state of equilibrium resulting mostly from biogeophysical processes that control the energy balance (i.e., partitioning between latent and sensible heat), and partly by biogeochemical processes involving trace gases and aerosols (see review from Spracklen et al., 2018); CO_2 absorption by the tropical forests, while extremely important, strictly depends on the water and energy fluxes (Spracklen et al., 2018).

Biogeophysical processes control surface thermal regulation, mediated by soil-vegetation fluxes of radiation, sensible heat, latent heat (moisture), and momentum to the atmosphere (Spracklen et al., 2018). Such exchanges depend on key land cover properties, such as the radiation reflectance (albedo), leaf area index (LAI, i.e., the leaf surface area per unit of shaded ground area), canopy structure, rooting depth, soil moisture availability, and photosynthetic capacity (P. J. Sellers, 1997). A key flux is the latent heat flux. Through the latent heat flux, the soil-plant system uses part of the net solar and thermal radiation to transform liquid water to vapor, in a process called evapotranspiration (ET). ET in tropical forests prevents overheating and helps to moisten and cool the microclimate, because net radiation is used primarily for ET instead of processes warming the environment (Ellison et al., 2017). This cooling effect is more efficient in tropical forests compared to other land covers such as urban areas, grasses, shrubs, nonirrigated crops, and other kinds of forests (Bonan, 2008).

Tropical forests usually have low albedo (~12%) compared with other land covers and thus are more efficient than other land cover types at absorbing radiation—a process controlled by soil and leaf reflectance and radiation trapping within the canopy. Despite the large capacity to absorb radiation in comparison with other land cover types, the structure of tropical forests (also known as surface parameters) help to transform energy by increasing ET and cooling the air. The surface roughness controls the wind shear at the canopy level and depends on the canopy architecture (e.g., height, distribution of LAI) and clumping; it generates turbulent mixing and contributes to the aerodynamic conductance, a property that favors air mixing, thus enhancing fluxes of water, heat, and momentum. Tropical forests have aerodynamic conductance higher than grasslands and crops by a factor of 2–10 (Spracklen et al., 2018). The high LAI of tropical forests (5–6 m^2m^{-2}) compared to crops and grasses (1–3 m^2m^{-2}) favors ET through the interception and evaporation of a larger amount of water in the leaves and through the enhancement of higher plant transpiration rates, since transpiration takes place through the leaves. As well, it has been suggested that ET is promoted in tropical forests by their large rooting depths in comparison with grasslands. In the Amazon, fine roots were found at depths greater than 10 m, while in grasslands, typical root depths are around 1 m (Nepstad et al., 1994). Deep roots are considered to play an important role in giving plants water access from the deeper and moister layers of the soil during dry periods (Bruno et al., 2006; Jipp et al., 1998; Nepstad et al., 1994). This helps to maintain elevated ET rates year-round, even during dry periods (Bruno et al., 2006), and also is considered a mechanism responsible for the maintenance of an evergreen forest.

Direct measures of ET using flux towers in Amazon forests and forest-savanna transitional areas reveal relatively weak seasonality, with small peaks occurring in different periods depending on the forest type. For the Amazon forest, higher ET was found in the dry season (3.9 mm d^{-1}) than in the wet season (2.8 mm d^{-1}; Table 4). By contrast, in Amazon forest-savanna transitional areas, dry season ET (3.3 mm d^{-1}) was lower than in the wet period (3.8 mm d^{-1}) (da Rocha, Manzi, Cabral, et al., 2009) (Table 4). The relatively weak seasonality in ET rates

Table 4
Seasonal Variability of Evapotranspiration (ET) in Various Biomes and Ecosystems in South America

Biome or ecosystem	Wet season ET (mm d^{-1})	Dry season ET (mm d^{-1})	References
Amazon Forest	2.8	3.2	da Rocha, Manzi, Cabral, et al. (2009) and da Rocha, Manzi, Shuttleworth, et al. (2009)
Savanna-forest transition	3.8	3.3	da Rocha, Manzi, Cabral, et al. (2009), da Rocha, Manzi, Shuttleworth, et al. (2009), and Cabral et al. (2015)
Brazilian Cerrado	3.7 (northern São Paulo) and 3.0 (Brasilia)	1.0 in both places	Cabral et al. (2015) and Quesada et al. (2008)
Seasonally flooded savanna (cerradão)	3.8	3.3	Borma et al. (2009), da Rocha, Manzi, Cabral, et al. (2009), and da Rocha, Manzi, Shuttleworth, et al. (2009)
Cerrado sensu stricto	–	1.9	Giambelluca et al. (2009)
Campo cerrado	–	1.4	Giambelucca et al. (2009)

and the slight increase in the dry season ET in Amazon forests have been attributed to an increase in the solar radiation along with having enough water to attend to atmospheric water demands (Shuttleworth, 1988).

On the other hand, in the Brazilian Cerrado biome, ET field measurements showed strong seasonality, with high ET values occurring in the wet period. In the wet season, local measures of ET varied from 3.7 mm d^{-1} in northern São Paulo (Cabral et al., 2015) to 3.0 mm d^{-1} in central-western Brasilia (Quesada et al., 2008). Dry season ET was about 1.0 mm d^{-1} in both places (Table 4). This seasonality in ET rates reflects the seasonality in the soil moisture content, which in the Brazilian Cerrado biome promotes leaf senescence in the dry periods. Giambelluca et al. (2009) reported eddy covariance measurements of ET for cerrado sensu stricto in the dry season (1.9 mm d^{-1}) equal to or greater than the measurements for campo cerrado vegetation (1.4 mm d^{-1}; Table 4), because in this period grasses generally become inactive. The ET over cerradão vegetation was higher than over other areas of savanna, especially for seasonal floodplain areas in the Brazilian Cerrado-Amazon Forest transition zone, where values of 3.8 mm d^{-1} in the wet season and 3.3 mm d^{-1} in the dry season were recorded (Table 4) (Borma et al., 2009; da Rocha, Manzi, Cabral, et al., 2009). These values approximate the ET rates of the Brazilian Cerrado-Amazon Forest transition, where ET values are slightly higher in the wet period than in the dry period. According to Borma et al. (2009), in the seasonally flooded savanna, the increase of ET rates in wet periods in comparison to dry periods was attributed to the evaporation of floodwater.

In relation to the thermal regulation, field observations using tall towers in Amazonian evergreen forests and pastures showed that, above canopy height, tropical forests had higher specific humidity (1–3 g kg^{-1}) during the afternoon, a lower diurnal temperature range with a cooler maximum temperature during the daytime (between 1.4°C and 3.0°C), and a warmer minimum nighttime temperature (between 0.8°C and 2.2°C), with differences in extremes peaking at 4°C for both daytime and nighttime (Culf et al., 1996). Direct measurements of ET with flux towers in the eastern Amazon corroborate the cooling mechanism of tropical forests: ET over pasture was lower than over forest by about 24%–39% in the wet season and even lower in the dry season (about 42%–51% lower) (da Rocha, Manzi, Shuttleworth, et al., 2009). In the southern Amazon, the difference was less pronounced: pasture ET was about 15% lower than tropical forest ET in the dry season, and the difference was not significant in the wet season.

It has long been known that diurnal temperature is lower at the ground level in canopy-shaded forest environments than in open areas. Even fragments of tropical forests may help to regulate air temperature below the canopy. For example, in the Atlantic Forest, in São Paulo state, researchers found that for each 1°C increase in maximum temperature outside of the forest fragments they studied, the increase in maximum temperature inside these fragments was only 0.38°C (Ewers & Banks-Leite, 2013).

Thermal regulation can also be expressed in terms of radiative surface temperature (*Ts*), measured with thermal infrared radiation detectors (e.g., satellites). *Ts* is directly related to plant leaf transpiration (Hesslerová et al., 2013), and it is usually higher than air temperature (*Ta*) during the daytime for clear sky conditions, although *Ts* and *Ta* are significantly correlated (Gallo et al., 2011). Estimates of ET with satellite models that utilize *Ts* showed a similar reduction of ET for land converted from tropical forest to pasture in the southern Amazon, varying from 28% (H. J. F. da Silva et al., 2019) to 40% (Khand et al., 2017) in the dry season, but insignificant in the wet season (H. J. F. da Silva et al., 2019). Similarly, for sparse pasture areas embedded in a large domain of Atlantic tropical forests, Wanderley and Miguel (2019) found that the average *Ts* increases nearly

proportionally to the anthropized area: each 25% increase of deforested area resulted in 1°C of warming, and that corresponded to approximate warming of about 4°C in *Ts* for the totally deforested area condition.

Based on these results, we conclude that in the more seasonal vegetation (i.e., savannas) and in grasslands, ET tends to decrease in the dry periods, making the cooling effect promoted by this vegetation less pronounced than in evergreen forests, such as the Amazon Forest. By maintaining elevated ET rates throughout the year, especially in the dry period, the Amazon Forest acts as a giant air conditioner that helps to cool the land surface far beyond its role in CO_2 absorption. The role of biodiversity in climate regulation services can be more easily understood by considering that biogeophysical processes (i.e., ecosystem functions) depend on key properties of the vegetation (i.e., land surface parameters), such as albedo, LAI, canopy architecture, and rooting depth (P. J. Sellers, 1997). These parameters are related to the structure of the tropical forests, which, indirectly, are related to the forest composition (i.e., species richness).

4.1.2. Rainfall Recycling and Moisture Transport

Besides acting as a thermal regulator of the air temperature through the consumption of net radiation that otherwise would increase the air temperature, tropical forests are efficient sources of water vapor to the atmosphere by ET (Dirmeyer et al., 2009; Keys et al., 2016, 2019; Van Der Ent et al., 2010). The rainfall over a terrestrial region is supplied by the condensation of atmospheric humidity originating from two sources: local ET and the horizontal upwind flux of water vapor (Eltahir & Bras, 1996). The water vapor locally generated by forests contributes to local rainfall, and a portion of this vapor is transported farther away by the atmospheric flow, contributing to rainfall in remote areas. Rainfall recycling and transport of water vapor to other basins through the atmospheric flow are considered valuable ESs (Keys et al., 2016, 2019; Van Der Ent et al., 2010).

4.1.2.1. Rainfall Recycling

In tropical forests, ET is generally high, resulting in high air humidity, and favoring convective unstable atmosphere and local rainfall (da Rocha, Manzi, Shuttleworth, et al., 2009; Rocha et al., 2015). The mechanism by which precipitation is produced from locally produced vapor (from evaporation and transpiration) is known as precipitation recycling. The rainfall recycling ratio (RR) is defined as the fraction of precipitation that originates from ET of a given region (Eltahir & Bras, 1996). The first estimates of recycling rates in the Amazon using stable water isotope measures suggested that about 50% of the rain in the Amazon basin originates from water recycled by the forest (Salati et al., 1979). Early numerical studies of atmospheric moisture recycling analyzed the ET sources and the precipitation sinks using Eulerian analytical models of vertically integrated atmospheric vapor balance in spatial boxes that estimated recycling rates within the same geographic region (Eltahir & Bras, 1994; Van Der Ent & Savenije, 2011; Van Der Ent et al., 2010). Later, other models (Lagrangian or Eulerian) used source-receptor relationships with moisture tracers to estimate trajectories for how ET over a specific area influences the amount of rainfall over another area (Gimeno et al., 2020). These numerical estimates showed that the percentage of global annual terrestrial precipitation originating from land ET is about 40%, and specifically for South America, estimates vary from below 10% (mostly in windward coastal areas or where winds move from ocean to land, such as in northeastern Brazil, in northern South America, and in Chile, in southwestern South America) to as much as 70% in central South America (eastern Peru and Bolivia, southern Amazonia, Paraguay, and the La Plata Basin [LPB]) (Gimeno et al., 2020; Van Der Ent & Savenije, 2011).

Van Der Ent et al. (2010) and Van Der Ent and Savenije (2011) showed the effects of spatial scale on recycling rates in South America with a scale-dependent atmospheric water budget model. In tropical and subtropical South America, they showed that the annual RR was lower at the 150 km scale (about 2%–6%) and higher at the 1,500 km scale (about 5%–20%). By contrast, Keys et al. (2016) calculated an index of the difference in moisture recycling between current vegetation and a hypothetical desert world, using both a land-surface biogeophysical model for ET and an atmospheric water budget model. In tropical and subtropical South America, they reported that the fraction of the precipitation regulated by land ET varies between 10% and 35%, which compares well with the previous estimates at the continental scale (Eltahir & Bras, 1994; Van Der Ent & Savenije, 2011; Van Der Ent et al., 2010).

Besides the provisioning of atmospheric vapor that ultimately forms rainfall, a contributing condition for rainfall production is the presence of cloud condensation nuclei (CCN). Research carried out under the Large-Scale Biosphere-Atmosphere Experiment in Amazonia regarding the physics of the Amazon climate demonstrates the

importance of these particles for the formation of clouds and rain in the Amazon. Trees emit volatile organic compounds (VOCs) into the atmosphere above the forest; in the absence of other aerosols, and mainly during the rainy season, VOC molecules form tiny crystals or aerosols that act as CCN. These aerosols attract a lot of water vapor, creating large, heavy raindrops, which may precipitate nearby (Chen et al., 2009; Pohlker et al., 2012; Poschl et al., 2010; S. Wang et al., 2016). In the Amazon's forests, potassium-salt-rich particles with clear biological origins also appear to be directly linked to cloud formation and precipitation (Pohlker et al., 2012).

Among the tropical forests, Amazonia hosts the largest contiguous block of tropical rain forest, and it is considered a particularly important contributor to ET (Choudhury et al., 1998). Combining remotely sensed data from tropical vegetation and precipitation with atmospheric transport patterns, Spracklen et al. (2012) found that over 60% of the Earth's surface (between 30°S and 30°N), the air that passes through extensive areas covered with vegetation produces at least twice as much rain as the air masses that cross extensive vegetated areas. It has also been shown that around 30%–50% of the precipitation that falls on the Amazon returns to the atmosphere in the form of water vapor produced by the forest itself (M. H. Costa & Foley, 1999; Salati et al., 1979; Wright et al., 2017). This vapor, continuously recycled, will contribute along with evaporated water from the oceans to the amount of rainfall that falls over the Amazon basin. The recycled vapor is also responsible for the large amount of water transported from the Amazon to the southern part of the continent through aerial rivers (Van Der Ent et al., 2010).

4.1.2.2. Moisture Transport to Remote Regions

Besides generating part of their own rainfall through rainfall recycling, forests inject moisture into the atmosphere that may be transported to other areas, contributing to rainfall in remote regions downwind, a mechanism that extends the forest influence to other regional and continental climate scales (Keys et al., 2016, 2019). In terms of moisture transport between nations, Dirmeyer et al. (2009) cataloged the main external suppliers of evaporative moisture for each nation worldwide. They found that nations that are upwind of a major low-level atmospheric circulation pattern are chief suppliers. This is the case, for example, with Brazil. Due to its large area, humid climate, and location in the continent (i.e., between the Andes and the Atlantic Ocean), Brazil is a major source of vapor to nearly every other nation in the South American continent. In a global context, Brazil is third in terms of its contribution of evaporative moisture externally. Brazil's largest contribution is to Paraguay, where Brazil is responsible for the generation of 40% of the country's total rainfall (Dirmeyer et al., 2009).

In South America, water evaporated from the tropical Atlantic Ocean is the most important source of humidity to the Amazon basin; this humidity is driven by easterly trade winds and directed inland with low tropospheric flow turning southward and moving along the east slopes of the Andes. As such, this flow can eventually contribute to rainfall in the southern Amazon and southward into the southern part of South America, with humidity often transported by the South American low-level jets (Drumond et al., 2014; Gimeno et al., 2020; Marengo et al., 2004; Van Der Ent et al., 2010). The southern Amazon (the states of Acre, Rondônia, and Mato Grosso) is a recognized source of vegetation-moisture recycling and precipitation to southern and eastern parts of the continent, including the LPB and the Brazilian states of Rio de Janeiro and Minas Gerais (Keys et al., 2016), which are among the most populated and developed regions in the country. The LPB is the second-largest basin in South America. The most developed economic region of southern Brazil is located there, and the basin also extends into Paraguay, Uruguay, and Argentina. To estimate the total percentage of precipitation over the LPB that originates from the Amazon basin, Zemp et al. (2014) used a Eulerian model less prone to issues of spatial scale, with novel parameterizations of re-evaporation cycles along the pathway, and estimated a mean annual value between 26% and 28%. Similarly, Martinez and Dominguez (2014) used a Lagrangian trajectory model and found a fraction of 20%, consistent with previous authors; they also determined that about 37% of the rainfall of the LPB comes from the oceans (southern Pacific and tropical Atlantic), 23% from local sources, and the remainder from other continental sources. The oceans rank first in providing moisture for rainfall over the LPB. However, ET of tropical Amazonian forests plays a substantial role comparable to the role of local sources, showing how important both local vegetation and the tropical Amazon forests are in controlling the regional rainfall of the LPB. These findings highlight the importance of ecological maintenance of regions that are potential sources of moisture to other regions.

4.1.3. Duration of the Rainy Season

Besides rainfall recycling and moisture transport, another process through which the Amazon forest helps in producing rainfall is through its role in triggering the wet season rainfall, thus modulating rainfall seasonality.

Modeling studies have shown that large-scale deforestation can increase temperature and decrease ET rates, with a potential reduction in precipitation (Feddema et al., 2005; Lawrence & Vandecar, 2015; Lejeune et al., 2015; Nobre et al., 1991; Sampaio et al., 2007; Spracklen & Garcia-Carreras, 2015). For simulations in which 100% of the rain forest is replaced by pasture, rainfall reduction was approximately 25% (Sampaio et al., 2021). That is because forest suppression directly impacts transpiration and ET processes, reducing the amount of vapor recycled by the forest and, consequently, the rainfall (e.g., Spracklen et al., 2018). Furthermore, the less energy (i.e., solar radiation) used to transform liquid water into water vapor, the more energy converted into sensible heat (e.g., Spracklen et al., 2018). It follows that a decrease in the amount of water vapor in the atmosphere will increase the air temperature. Another climatic impact arising from Amazon deforestation is lengthening of the dry period. This can be very harmful for human populations since it increases the period when local populations rely on water reserves. An increase in the length of the dry season together with an increase of fire occurrence is considered to be one of the most impactful drivers of change in forest structure and composition.

The first study to suggest that the duration of the dry season could be affected by changes in land cover was a climate modeling study by M. H. Costa and Pires (2010). They demonstrated that both Amazon and Brazilian Cerrado deforestation contribute to an increase in dry season duration in the area known as the arc-of-deforestation. Thus, combining the effects of both the Amazon and Brazilian Cerrado deforestation scenarios, the dry season may increase from 5 to 6 months.

Observational evidence was provided by Butt et al. (2011), who analyzed trends in the onset of the rainy season in the state of Rondônia, western Brazil, a region that has been continuously experiencing deforestation since the 1970s. They found that delaying trends may be as great as 0.6 days per year, and after 30 years of deforestation, the onset of the rainy season is expected to be 18 days later.

The mechanism by which the rain forest influences the onset of the rainy season has been explained by Fu et al. (2013). The high moisture fluxes from rain forest transpiration injected into the atmosphere during the dry season stimulate an earlier onset of the wet season than would be expected from atmospheric dynamics alone. Specifically, rain forest transpiration increases shallow convection that moistens and destabilizes the atmosphere during the initial stages of the dry- to wet-season transition, conditioning the regional atmosphere for a rapid increase in rain-bearing deep convection. In turn, this process drives moisture convergence and wet season onset 2–3 months before the arrival of the Amazon Convergence Zone (Fu et al., 2013; Wright et al., 2017). Recent evidence using both rain gauge and Tropical Rainfall Measuring Mission data empirically demonstrates the role of rain forests in several critical features of the southern Amazon rainy season. Leite-Filho et al. (2019) have shown that forest presence is associated with an earlier onset and late end of the rainy season, leading to a long rainy season. Moreover, Leite-Filho et al. (2019) have shown that higher forest cover is associated with a low frequency of dry spells of any duration in September, October, April, and May, the transition months between the dry and the rainy seasons. In other words, in well-preserved areas, the rainy season begins earlier and is less likely to be interrupted by a long dry spell in its initial days. However, in heavily deforested areas, the rainy season starts late and is more likely to be interrupted by a long dry spell.

4.2. Water Cycle Regulation

The importance of tropical forests goes far beyond their role in climate regulation through the previously described biogeochemical and biogeophysical processes; tropical forests have intrinsic ecohydrological mechanisms that help to regulate the amount, quality, and timing of water that flows over and through the land surface down to the stream. Some ESs derived from these ecohydrological processes are more well-established than others. For example, there is high confidence and good agreement between researchers and practitioners about the role of the forests in controlling erosion and their role in maintaining water quality. Both ESs are favored by the high infiltration rates promoted by mature tropical forests (Figure 3). While runoff erodes the soil, carrying soil particles and nutrients (or contaminants) over the land surface towards water bodies downstream, water flow through the soil profile filters and buffers any eventual contaminant load (or nutrient) in the infiltrated water. Through these processes, tropical forests improve both soil and water quality.

On the other hand, more controversial is the role of tropical forests in controlling or preventing landslides, flash floods, and debris flow. These processes result from the large stormflows typical of tropical areas. Large amounts of water falling on the land surface in a short time (minutes to hours) may exceed the capacity of the soil-forest system to absorb water (the sponge effect), thus promoting landslides, debris flow, and flash floods in the most

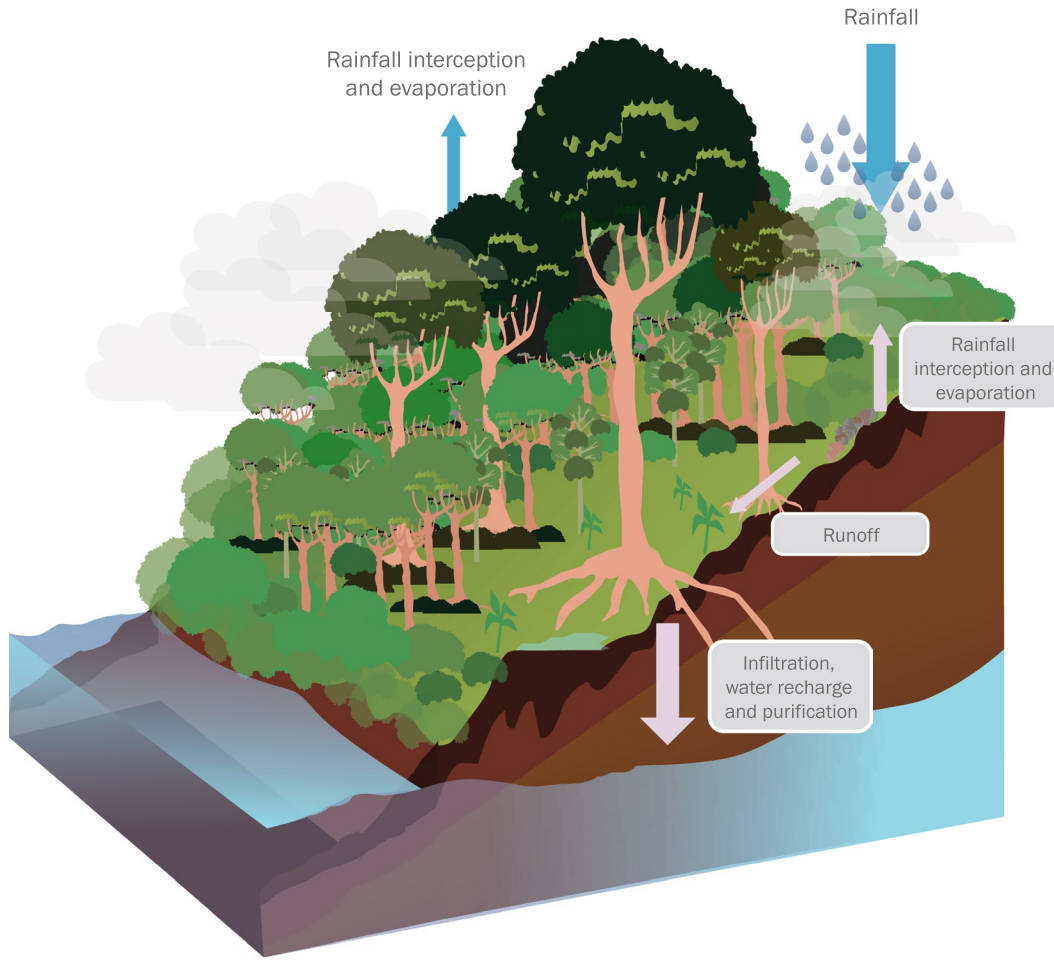

Figure 3. The roles of tropical rain forest components in the hydrological cycle.

susceptible or vulnerable areas. One of the consequences of global climate change is an increase in the frequency and severity of extreme climatic events, such as severe storms and droughts (IPCC, 2021). In this sense, while the forests may not always directly buffer the effects of extreme climate events, they may indirectly help to moderate these effects by mitigating anthropogenic global climate change. Another controversial claim about the role of forests in the water cycle regards their capacity to recharge ground and surface reservoirs. Given the high ET rates of tropical forests (Table 4), questions have been raised about the capacity of these forests to favor water infiltration in quantities large enough to support their own use and, at the same time, recharge the groundwater reservoir. Considerations about the ecohydrological role of tropical forests in these water regulating services are presented below.

4.2.1. Soil Erosion and Water Quality

Soil erosion is the physical process of topsoil breakup and removal by erosive agents such as water and wind (Lal, 2001). Throughout geological timescales, erosion processes have shaped natural landscapes. Historically, human activities (e.g., tillage, logging) have accelerated erosion, increased soil degradation (e.g., nutrient loss), decreased water quality (Lal, 2001; Pimentel & Kounang, 1998), and decreased soil fertility.

Depending on rainfall intensity, soil type, moisture condition, slope of the terrain, and the existence and type of vegetation cover (i.e., its structure and composition), rapid surface flow has a high potential to generate erosion and carry sediments and nutrients (Kundzewicz et al., 2014; Pokhrel et al., 2018). Erosion carries nutrients and organic matter, essential components of soil fertility. In addition, excess nutrients and sediments in water bodies may compromise the dissolved oxygen levels and light penetration, which are fundamental for organisms' survival and growth, and they may harm water quality in general.

Water purification and erosion control are perhaps the most recognized regulating ESs related to tropical forests (Anache et al., 2017, 2019; Bruijnzeel, 2004). The erosion caused by raindrop impact on the soil is mitigated by the dense canopy and surface litter that intercept precipitation, store rainwater before it evaporates back to the atmosphere, and reduce the size and kinetic energy at which these drops reach the soil surface (Bathurst et al., 2011; Levia et al., 2017). The topsoil in tropical forests has a litter layer, high organic matter content, high porosity, and diverse micro- and macroorganisms living in a dense root system that facilitates water infiltration. Altogether, these processes also favor the water quality of the water bodies located downstream from the flow path. Besides filtering pollutants and retaining nutrients, riparian forests benefit adjacent water bodies by cooling temperatures and maintaining adequate microclimates for the aquatic environment (Cassatti, 2010). Evidence in Brazil shows that natural forest areas have rates of soil loss significantly lower (0–1.5 t ha^{-1} y^{-1}) than areas of fallow, grass, and croplands (up to 193.2 t ha^{-1} y^{-1}) (Anache et al., 2017). Soil loss in protected areas, such as in riparian forests, substantially reduces total soil losses (9–20 t ha^{-1} y^{-1}), mitigating flooding, sedimentation, and nutrient runoff in farmland in all Brazilian biomes (Mayer et al., 2007; I. A. Silva et al., 2011; Tabacchi et al., 2000).

The contribution areas for hydropower reservoirs covered by intact remnants of the Atlantic Forest presented more acceptable eutrophication indicators (nutrients, electrical conductivity, and pH) than areas covered by pasture and croplands. In the Sarapuí River Basin, Rio de Janeiro state, Brazil, water quality was significantly better in forested regions (Atlantic Forest) compared to agricultural lands, exhibiting 99% lower fecal coliform concentrations, 40% less nitrogen, and 58% less phosphorus (de Mello et al., 2018). Water from springs in forest remnants also shows better indicator values, such as lower nitrite and nitrate concentrations and more neutral pH than water in agricultural lands (Marmontel et al., 2018). However, forest fragmentation and degradation compromise the ability of forests to reduce the amount of sediment, total nitrogen, and total phosphorus and to regulate pH and water temperature (de Mello et al., 2017, 2018).

4.2.2. Slope Stabilization

Landslides and flash floods mainly occur in areas with high slopes under heavy precipitation. In South America, the flood control regulating service is more important in the Andes and the Atlantic Forest. In the Atlantic Forest biome, relief often features hills and steep slopes along regional mountain ranges (Bruijnzeel, Kappelle, et al., 2011). The climate is wet in the summer and strongly influenced by South Atlantic convergence zone, which favors intense rainfall and/or persistent rainy days with high rainfall volumes that increase the likelihood of erosion and shallow landslides in vulnerable areas. These conditions, combined with the prevalence of densely occupied and highly anthropized areas increase the risk of natural disasters. Several authors have reported anomalous extreme events with hydrological peaks in southeastern Brazil over recent decades (Doyle & Barros, 2011; Maciel et al., 2013; Saurral et al., 2008). Similar conditions are found in Southeast Asia, where heavy monsoon rains may cause significant flooding events. For example, in five years (2003–2007), 11 major flood events affected Nepal, Indonesia, Sri Lanka, Bangladesh, India, and Thailand, affecting 65 million people and killing over 3,700 people (Zafirah et al., 2017). Many of these events were caused by the failure of barriers (forests, riparian zones, and infrastructure).

Soil mass movements are defined as masses of soil sliding due to gravity action (Sidle & Ochiai, 2013). They comprise erosive processes, landslides, and debris flow. Mass movements can occur at the terrain surface, as is the case with erosion processes and debris flow. They can also occur a few meters below the surface, along a sliding surface (failure surface), which can be flat or concave depending on the soil type and geologic formation. In general, surface mass movements such as erosive processes and debris flows cover large areas, whereas landslides are generally more restricted to a given slope. However, due to the large volumes of moving soil mass, landslides may impact large areas downstream. The influence of vegetation over these processes varies according to the mass movement type. As presented before, the influence of tropical forests on erosion processes is well established. However, the influence of tropical forests on mass movements such as landslides and debris flow is more controversial and depends on several factors, as discussed below.

The influence of vegetation on slope stabilization can be seen through hydrological or mechanical processes (Ghestem et al., 2011). The hydrological mechanisms are associated with the water flow in and out of the soil profile (respectively, infiltration and ET; Figure 3); the water content (i.e., ratio between water volume and soil volume) resulting from this flow; and the influence of the moisture content on the pore-water pressures, that is, the pressure that the soil water exerts on the soil matrix, potentially aggregating or destabilizing the soil mass.

Negative pore pressures, or suction, developed in nonsaturated soils tend to favor slope stability, while positive pore pressures, developed during infiltration, act to destabilize the soil mass. Soil saturation—that is, the filling of the void spaces with water—decreases suction, which is an aggregating element, and increases the weight of the soil mass, promoting its destabilization and tendency to fall by gravity. Mechanical processes are related to shear strength, that is, the resistance that the soil offers to rupture of the soil mass. In general, mechanical and hydrological processes have been studied separately in soil mechanics. But to understand the role of vegetation in slope stabilization, both mechanisms—mechanical and hydrological—must be considered together (Ghestem et al., 2011).

Regarding the role of vegetation from a mechanical point of view, some studies suggest that the weight of trees, particularly under the action of winds and storms, can act as a destabilizing mechanism for the slope. On the other hand, some studies have suggested that the roots could act as a stabilizing element, increasing the shear strength in areas of high root concentration. However, from the hydrological point of view, roots can also work as channels that drive water quickly inside the land mass (De Oliveira Marques et al., 2018; Fattet et al., 2011; Ghestem et al., 2011), promoting fast saturation, cohesion loss, and rupture (Lacerda et al., 2014).

Marques et al. (2018) analyzed the influence of the roots of two land cover types—secondary tropical rain forest and pasture—on the ecohydrological behavior of the slopes of the Atlantic Forest in Serra do Mar. They found that, in the forest, the concentration of thick roots occurred along the entire instrumented soil profile (220 cm), and decreased with depth; in the pastures, the thick roots were concentrated only at the surface (i.e., a few centimeters below the soil surface). The biomass of fine roots was similar between the areas, the main difference being observed in the rooting depth—while in the pasture the maximum rooting depth was 100 cm, in the forest roots were found up to 200 cm deep. With regard to pore pressures, the study showed that suction accompanies precipitation, as expected, but the amplitudes of variation were greater in the forest than in the pasture. According to these authors, both vegetation cover types favored soil saturation. However, in the pasture, soil saturation occurred in the first 50 cm, while in the forest, soil saturation occurred at greater depths—100, 150, and 220 cm, depending on the rainfall event. Positive correlations were found between soil saturation depths and the maximum depths of roots in the forest and pasture. According to the authors, these results could explain why landslides in the Atlantic Forests tend to be deeper than landslides in grasslands and pastures (Avelar et al., 2013; Coelho Netto, 2005; Salemi et al., 2012). However, there is still a need to investigate whether landslides are generally more likely to occur in pastures and grasslands than in forested areas. In addition, rainwater infiltration, despite being a factor that in some circumstances may trigger soil saturation and, eventually, landslides in very steep areas, is also a fundamental process through which forests help to promote water infiltration and groundwater recharge. Substantial research is still necessary to truly understand the role of these forests in slope stabilization. Besides, as Lefcheck et al. (2015) argued in relation to biodiversity, we should not focus only on one service or function but on the multifunctionality of forests for an uncountable number of services.

4.2.3. Flash Flood Control

Flash floods are another consequence of the ecohydrological processes that occur in tropical forest ecosystems. The water that does not infiltrate the soil is routed to overland flow. Overland flow is the rapid water flow that reaches water bodies (rivers, lakes, bogs, and swamps) during or slightly after a rainfall event, and which may result in flash floods in the lowlands. Similar to what happens with landslides, flash floods strongly impact downstream areas, promoting damage, deaths, and economic losses in the regions affected. Historically, the Atlantic Forest region has experienced particularly intense flash flood events of great magnitude (IPCC, 2021; Scott et al., 2005).

The role of tropical forests in controlling flash floods can be viewed as the flip side of the role of tropical forests in controlling water infiltration, groundwater recharge, and water purification processes. The water that does not infiltrate the soil will otherwise run off superficially. If the rainfall is extremely intense and strong such that it surpasses the infiltration mechanisms, this water will flow overland. In areas with less-dense cover, this overflow can carry solid material, promoting soil erosion and nutrient leaching. In some cases, the rainfall is so strong that both surface and subsurface runoff destabilize and disaggregate the upper layers of the terrain, promoting highly damaging debris flow.

Flash floods are events at the very tail end of the flow frequency distribution, with magnitude exceeding the channel capacity, with a return interval $\geq$10 years, and during which most of the sediment is transported. There is long-held opinion that deforestation leads to increasing peak flows, as it generally disturbs water storages that

retain liquid water (e.g., canopy, forest floor, microrelief, and soil column) and reduces the concentration time (time needed for water to flow from the most remote point to the outlet of a watershed) upon shifting dominant quick flow from subsurface stormflow to overland stormflow (Andréassian, 2004; Runyan & D'Odorico, 2016). The most impactful peak flows are likely to occur in areas with low infiltration capacity caused by soil compaction, that is, roads and where streams were modified with increased channel width and decreased water column due to erosion and siltation (Dose & Roper, 1994). For a small catchment, Waterloo et al. (2007) found evidence of forest reducing peak flows under intense rainfall that produced flash floods. On the other hand, several past studies showed that logging forests without disturbing the forest floor did not impact the peak flows, and rather it only increased the smallest peaks following the driest antecedent conditions (Ziemer, 1998). Even with hydraulic conditions adequate for infiltration, as they are in tropical forests, it appears that the soil layers probably do not have sufficient capacity to accommodate large amounts of rainfall and therefore end up flooding (Scott et al., 2005).

Hewlett (1982) analyzed many forest regions, generally small basins, and concluded that the effect of forest operations on the magnitude of major floods was minor compared to variability of rainfall and basin storage. Small basins are considered to be more sensitive to surficial disturbances, as hillslope processes control the stormflow response to rainfall; this is different from in large basins, where responses are much driven by the geomorphology of the channel network. Notwithstanding this, a worldwide analysis by Zhang et al. (2017) found that the increase in annual runoff does depend on forest cover loss at multiple spatial scales, whereas the effect of forest cover gain is inconsistent, and also that the sensitivity to forest cover change attenuates with basin size only in large watersheds. Chagas and Chaffe (2018) analyzed 36 years of data from hundreds of rainfall and flow gauges in southern Brazil and reported widespread temporal trends, mostly constrained to watersheds smaller than 10,000 km^2; in general, they showed that rainfall did not directly translate into changes in streamflow. Changes in the annual maximum flows of forested basins were not significant even for a substantial increase of annual and maximum rainfall. However, changes in precipitation and streamflow were correlated for two indices (duration of low-magnitude events and seasonality) for agricultural basins only, which suggests that nonforest land cover could be more sensitive to changes in the rainfall regime. The authors suggested that the relationships of forest or agricultural basins to streamflow changes in the Atlantic Forest biome need additional study. So, despite the number of studies published, it is still unclear how much credit should be attributed to land cover versus climate for controlling streamflow variability.

4.2.4. Water Provisioning

While the role of tropical forests in the maintenance of water quality is well recognized (they mitigate erosion and buffer contaminant loads from upland areas), the same is not true for their role in terms of water quantity. In the face of the large ET rates measured for tropical forests (at around 3–4 mm d^{-1}, which totals to approximately 1,000–1,500 mm yr^{-1}), there is a common belief that tropical forests demand more water than other land cover types (Bruijnzeel, 2004), thus reducing infiltration and runoff and consequently competing with humans for water resources (Andréassian, 2004; Bruijnzeel, 2004). Several studies in South America's tropical forests have dealt with the influence of land cover change and deforestation on runoff production. Most were conducted in paired catchments with similar climate and terrain characteristics, such as basin size and format. We have identified only four paired forest/pasture studies that have looked at water balance in small watersheds across Amazon terra firme forests. These studies showed greater mean runoff coefficient values (a measure of discharge after rainfall) in pastures compared to forests: 21% versus 43% in Manaus, 3% versus 17% in Paragominas, 12% versus 19% in Novo Progresso, and 1% versus 17% in Rondônia (Chaves et al., 2008; Guzha et al., 2015; Tomasella et al., 2008; Trancoso, 2006). These results suggest that, as expected, forests are more efficient in favoring water transpiration and infiltration (i.e., decreasing or slowing down the water flux to the rivers). In contrast, in the pasturelands, runoff is favored. Since the water readily available for human use is stored in rivers and reservoirs, the quick runoff was translated into more water availability in deforested areas (pastures) than in forested ones. However, it is important to mention that this demand-side perspective of tropical forests in terms of water availability is simplistic and neglects the role of tropical forests in producing water vapor and rainfall through ET (see Section 4.1). That is probably because, according to Keys et al. (2016, 2019), water vapor is an invisible ES for most people.

Another important point to consider when analyzing the influence of tropical forests on water quantity is that the trade-off between infiltration and ET in a given region depends on many other factors that paired catchments

have not accounted for. Concerning infiltration, forests and litterfall have a well-documented role in buffering the impact of heavy rainfall by absorbing, distributing, and channeling the water into the soil (Figure 3). Infiltration rates are also a function of slope, soil porosity, the distribution of soil pore sizes, development of biopores at the soil surface, and how well water percolates inside the soil (e.g., through preferential flow) (Beven & Germann, 2013; Fattet et al., 2011; Ghestem et al., 2011; Joffre & Rambal, 1988). These soil properties and conditions have significant spatial variability, even inside a small catchment. Concerning ET, which is largely controlled by plant transpiration (Jasechko et al., 2013), rates depend on tree density, fraction of vegetated area, and plant hydraulic traits (Sperry & Tyree, 1988), which determine sap flux density and the volume of transpired water and vary by forest type (Kunert et al., 2017). Another factor that affects ET rates is forest age. Pioneer trees and trees used in the first stages of reforestation are usually fast-growing and thus have high transpiration rates. Attention to this type of forest may have contributed to the common notion that all forests have heavy demand for water (Tabarelli et al., 2010). However, much more needs to be known about the ecohydrological behavior of tropical forests before generalizations can be made about these highly biodiverse regions in terms of their role in freshwater provisioning. For example, in the Brazilian Cerrado, where there is a prolonged dry season—at least five months—water infiltration through the roots has been considered an important mechanism to recharge the groundwater (Klink et al., 2020).

Another point frequently neglected in analyzing the role of tropical forests in water provisioning is related to cloud forests. Cloud forests are found near shoreline plateaus and crests of mountain ranges in the Atlantic Forest biome and can be called natural water reservoirs (Bruijnzeel, Kappelle, et al., 2011). They help promote the ESs of maintaining water quantity, water quality, and landmass stability (Bruijnzeel, Mulligan, et al., 2011). The combination of dense-canopy cloud forests with a very humid climate tends to saturate the air with water vapor, decreasing ET and increasing soil infiltration. Reductions in ET may amount to over 20% of rainfall and even up to around 50% in some cases (Bruijnzeel, Kappelle, et al., 2011; Hamilton, 2009). Long-term hydrological measurements in Atlantic cloud forests of southeastern Brazil with a mean rainfall of 2,100 mm yr^{-1} showed 70% of rainfall partitioned as streamflow (11% of which was stormflow) and 30% as ET (Fujieda et al., 1997). Salemi et al. (2013) studied three small catchments with different land covers (montane cloud forest, pasture, and eucalyptus) for 2 years in the Atlantic Forest of southeastern Brazil. They observed overland flows in the three areas, with no perched water table and the runoff mechanisms apparently dominated by vertical flow paths (Figure 3). They measured greater saturated hydraulic conductivity near the surface and less overland flow in the forest than in the other land covers. Interestingly, the authors found the mean streamflow of the cloud forest and pasture to be similar, and both were slightly lower than eucalyptus streamflow.

Considering the complex dynamics affecting water provisioning by tropical forests and the conflicting opinions about this topic, there is an urgent need to better address the role of tropical forests in influencing the water balance and freshwater production. This discussion is critical for the Atlantic Forest biome, where most of the Brazilian population resides. Several forest conservation and restoration programs have been developed to recover the ESs of water provisioning (Taffarello et al., 2017). Additionally, under the Paris Agreement, several countries have committed to restoring forests to minimize CO_2 emissions and mitigate global changes. However, while there is a consensus about the role of tropical forests in climate regulation, provision of clean water, erosion control, and flood mitigation, not enough is known about the ecohydrological behavior of tropical forests and the trade-off between water infiltration and forest transpiration.

5. Tropical Forests and Provisioning Services

According to the Brazilian ESs Law (Brasil, 2021), provisioning services are "those that provide environmental goods or products used by human beings for consumption or commercialization, such as water, food, wood, fibers and extracts, among others." In most cases, the direct value of forest products to people relates to the characteristics of the specific species, so that provisioning services are more directly related to the composition (i.e., species richness) of the tropical forests than to the structure and function attributes. They are also strongly related to the culture, heritage, and knowledge of local peoples (see Section 6). However, since the availability of these services is seasonal and related to the climate, they are also indirectly related to climate patterns, which in turn depend on the tropical forests' structure and functions. Since our focus is mainly on the services rather than on the goods provided by the ecosystem, we present just two types of provisioning services as examples—provision of wild foods for local consumption and trade and provision of medicinals—both of which are nontimber forest products.

5.1. Tropical Forest Wild Foods for Local Consumption and Trade

For traditional communities, wild foods are extremely important for subsistence, serving both as a main source of protein and as a food supplement, as well as an important income source. Access to diverse forest foods, especially fruits and vegetables, is crucial for supplying necessary micronutrients. Foods such as fish, meat, fruits, and seeds are traded in local or outer markets to augment family income (A. L. da Silva & Begossi, 2009; Ortiz et al., 2013). In the Brazilian Amazon, a study carried out with farming families in the Rio Capim region, in the state of Pará, showed that for 1 year, products obtained from the forest, such as fruits, vines, and even game, were equivalent to 25% of family income. Of the total of these products consumed by families, the forest provided 87% of all the fruits consumed, 85% of the vines, and 82% of the game (Shanley & Medina, 2005).

The seasons have an important influence on the phenology of several species, determining the periods of flowering and fruiting, and therefore shaping people's food consumption patterns and market prices. For instance, in the Amazon, the Brazil nut (*Bertholletia excelsa*) has peak production during the rainy season, influencing dynamics of extractive communities (Tonini & Pedrozo, 2014). Similarly, the extraction of cupuaçu (*Theobroma grandiflorum*) and açaí (*Euterpe oleracea*) varies with subregional climatic and geographical characteristics (Homma et al., 2006). For açaí, the off-season periods influence the price of the product and consumption patterns even in large cities such as Amazonian state capitals, where açaí is one of the main elements of the diet (Bezerra et al., 2016; Homma et al., 2006). Consumption patterns of riverine populations, who have fishing as their main source of protein, are even more dependent on the seasons. For instance, fish and chelonian (turtle) consumption increase in the dry season, while bushmeat (meat from hunting) and fruit consumption increase in the rainy seasons (A. L. da Silva & Begossi, 2009). In Amazonian várzea, the planting period begins at the end of the flooding season. Once the flooding restarts, local communities complement their food sources by foraging and hunting in the forests (Adams et al., 2005). Although fishes are not directly related to forests, the present of forests help to maintain river water quality (see Section 4.2.1). Forests can also provide food (fruits and seeds) and habitat to fishes (Arantes et al., 2018).

In the South American tropical savanna, among the 100+ native species providing humans tasty and nutritious fruits (Pereira et al., 2012), *pequi* fruit (*Caryocar brasiliense*) stands out. Pequi plant is endemic to the Brazilian Cerrado and is in an early stage of domestication (Sousa Júnior et al., 2018). Its fruit is used for food and oil, with great economic relevance for traditional peoples (Sousa Júnior et al., 2013).

ESs influence the economy in various ways. Local communities, including Indigenous Peoples and others who live close to or inside forests, obtain direct and indirect benefits from these forests that economically sustain their livelihoods, mainly from environmentally friendly agroforestry systems. It has been shown that agroforestry preserves most of the goods provided by the forests, while monocultures are often associated with the depreciation of forest composition and structure, impacting ecosystem functions and, consequently, ESs provision. The reduction of ESs provision affects beneficiaries and agricultural systems both near and far from the forests providing these services (Cotta, 2017; Humphries et al., 2020; Torres et al., 2015).

5.2. Provision of Medicinal Products

Tropical flora diversity is valued not only for its use as food, firewood, and building materials, but also for other important cultural and ritual uses, including medicines (R. Vieira & Martins, 2000). Of the phanerogamic families (i.e., plants that produce seeds) listed for the Cerrado of Mato Grosso, about 56% are medicinal species (R. C. Mendonça et al., 2008). Their uses include anti-inflammatory (De Castro Peixoto et al., 2019), gastroprotective (Luiz-Ferreira et al., 2010), oncological (Mousinho et al., 2011), and wound-healing (Ribeiro Neto et al., 2020) applications. Other examples include the species *Lippia microphylla* and *Dimorphandra gardneriana*, common in the Brazilian Cerrado, which each have a considerable protective factor against ultraviolet rays (SPF of 26.82 and 20.12, respectively), demonstrating great potential for the pharmaceutical and cosmetic industries due to the high presence of sakuranetin flavonoids and quercetin glycosides (Nunes et al., 2018).

In the Amazon, species historically used in traditional medicines such as Copaíba (*Copaifera officinalis* L.) and Andiroba (*Carapa guianensis Aubl.*), have been adopted by the pharmaceutical and cosmetics industries (A. P. Mendonça & Ferraz, 2007; C. D. B. Ribeiro et al., 2021; Pennaforte, 2003). Other products provide materials and inputs for biochemicals and medicines exported worldwide. The region produces oils with larvicidal activity against the *Aedes aegypti* mosquito, which is the vector of dengue and chikungunya, two tropical diseases

that yet lack effective treatments and vaccines (C. N. Dias et al., 2015). The Amazon also is home to some fungi species with potential as natural dyes for pigmentation (Celestinodos et al., 2014).

In the Atlantic Forest, about 630 plants have been found to exhibit some medicinal value (V. B. Oliveira et al., 2012) to treat conditions such as central nervous system disorders, pain, low immunity, inflammation, and respiratory and gastrointestinal diseases (Dutra et al., 2016). For instance, after many studies focusing on the anti-inflammatory effects of *Cordia verbenacea* (Maria-milagrosa) (Sertié et al., 2005), a collaboration between academia and industry resulted in the development of an important analgesic and anti-inflammatory medicine (Dutra et al., 2016). In the state of Minas Gerais, a semi-structured interview with 62 local healers (*raizeiros*) identified 264 medicinal plants with hundreds of potential uses to treat problems such as heart and intestinal diseases, kidney problems, fever, and pain (J. E. Dias & Laureano, 2009). Fauna can also be used in the development of new medicines. One example is captopril, a medicine used worldwide to treat hypertension; its development was based on the isolation of a protein found in the venom of a South American pit viper, *Bothrops jararaca* (Cushman & Ondetti, 1991). In the Amazon region alone, it is estimated that around 580 animal species are used in traditional medicine (Alves & Alves, 2011).

6. Tropical Forests and Cultural Services

According to the Brazilian ESs Law (Brasil, 2021), cultural services encompass "the nonmaterial ESs, such as recreation, tourism, cultural identity, spiritual and esthetic assets, and knowledge." For traditional communities, the relevant characteristics of local ecosystems and how they function are strongly related to the community's origins and worldview and how its members transfer their knowledge across generations (Diegues, 2019). In this context, natural places can take on sacred and symbolic values that are crucial to the establishment of social identity and sense of place (Costanza et al., 2017; Milcu et al., 2013). Nonmaterial benefits can be used by different groups and societies for recreational, tourism, and educational purposes, contributing to awareness of the importance of the forest and, consequently, to its conservation. Here, we highlight, as examples of cultural services, cultural identity, knowledge production, and human health.

6.1. Tropical Forests, Cultural Identity, and Knowledge Production

Perception of the value of forests varies significantly among different peoples due to their different knowledge and value systems (Joly et al., 2019). For many South American Indigenous Peoples, their environments, economies, and belief systems are wholly integrated (Brondizio et al., 2009). Even tangible ESs, such as providing fresh meals, medicinals, and other goods, may also have spiritual and cultural value (Joly et al., 2019). The subjectivity of cultural services is also evident when evaluating ecotourism and the different benefits of natural areas.

Many traditional communities have explored nature in a sustainable manner for millennia, through which they transfer knowledge, habits, and beliefs and reaffirm their identities and forms of social organization (Diegues, 2019; T. P. da Silva et al., 2020). Some areas of traditional knowledge include food production, medicinal applications, and fire management methods, among others. For example, collection of Brazil nuts (*B. excelsa*) for traditional communities depends on knowledge of practices transferred between generations regarding storage, consumption, and even commercialization (Barbosa & Moret, 2016; T. P. da Silva et al., 2020). The same is true for products with high commercial value, such as wood, cocoa (*Theobroma cacao* L.), and açaí (*E. oleracea* Mart.) (Homma, 2014).

Regarding fire management, conflicts have emerged in recent decades in Brazil that are indicative of different cultural perspectives toward fire and its management. Widespread fires by large-scale commodity producers that burned vast amounts of biomass (Pivello, 2011) and incorrect attribution of deforestation and CO_2 emissions to cultural and hunting fire use by Indigenous Peoples (Welch et al., 2013) both contributed to creation of a no-fire policy in Brazil (Durigan & Ratter, 2016), even in fire-prone Brazilian Cerrado ecosystems (Simon & Pennington, 2012). In fact, traditional peoples of savanna regions learned by experience how to manage fire to maintain ecosystem properties (Durigan & Ratter, 2016). A study shows that local pastoral fire management prevents the spread of wildfires (Eloy et al., 2019). Satellite imagery of fire scars in an area of integrated fire management by local communities was compared to nearby sites where a fire suppression policy has been enforced. The results demonstrate that community-managed areas suffered less damage (Eloy et al., 2019).

The territories of the Peruvian and Ecuadorian Amazon River headwaters also offer important examples of cultural services. More than 500,000 Indigenous people of different ethnicities and nationalities recognize the

ecosystem and its benefits broadly and systemically as the basis of their physical and spiritual survival, essential to the maintenance of their languages and customs across generations. Based on this understanding, Indigenous Peoples have been engaged in struggles against the destruction of forests—primarily through the exploitation of oil and gas—and the maintenance of their sacred spaces in the cradle of the Amazon River (Etchart & Cerda, 2020).

Biocultural diversity in the Atlantic Forest includes a remarkable array of Indigenous and traditional groups, such as the people known as *caiçaras*, *jangadeiros*, *quilombolas*, and *caipiras*, who hold significant traditional knowledge of the diverse ways of life in the forest (Diegues, 2019). Millennia of historical management by Atlantic Forest peoples have contributed to the diversity and structure of the forests (R. R. de Oliveira, 2007). Since colonization, a long history of intensive anthropogenic activity has transformed these Atlantic Forest landscapes, modifying the quantity and quality of the forest services supplied for people and nature (Leal & Câmara, 2003). In this sense, to truly understand the types of cultural services and the value they hold for different local and nonlocal communities, effort is needed to contact, communicate with, and learn from people directly. Although awareness of the importance of natural areas for human physical and mental health has increased, especially in a post-COVID-19-pandemic context (Yin et al., 2021), cultural ESs are still the least studied category of ESs and the most difficult to insert into public policies and decision-making (van der Hoff et al., 2022).

6.2. Tropical Forests and Human Health

Forest ecosystems provide multiple services directly or indirectly linked to human health and well-being (World Health Organization, 2005). Some of the relevant ESs (varying across locations and beneficiaries) include regulation of nutritional quality, provision of dietary diversity, maintenance of nutritional well-being, maintenance of food security, maintenance of mental health, disease control, and regulation of thermal comfort.

Human populations have disconnected from nature since they have been moving into cities, which has affected their physical and mental health, emotional well-being, and personal and social skills (Fuller et al., 2007; Miller, 2005). Impacts on health include not only traditional communities losing their sense of the social identity associated with the landscape (Milcu et al., 2013), but also impacts on urban populations via the lack of human-nature relationships (Sandifer et al., 2015). Beyond air purification and temperature mitigation (Andersson et al., 2015), contact with nature can provide a sense of well-being that is important for mental health and leisure, increasing the quality of life in urban areas, at the same time as contributing to the purpose of education and awareness about the importance of nature for humans (Annerstedt Van Den Bosch & Depledge, 2015; Tiriba & Profice, 2019). Human demand for contact with nature, the contemplation of natural scenic beauty, and even the search for spiritual connection are representations of cultural ESs that can also be incorporated into the tourism sector; in this way, they represent activities of great economic potential that can constitute a source of income for communities that inhabit and maintain natural landscapes, as well as for the maintenance of public green areas (Cooper et al., 2016).

It is also important to mention that the provision of medicinal resources is only possible due to systems of long-term nonscientific knowledge transfer. An example relates to 115 plants used by the traditional Wichí people of the northern Argentinian Chaco; these plants collectively offer about 400 medicinal applications. Knowledge of many of these applications originated from the Wichí people's long-standing contact with Criollos, another traditional regional people (Suárez, 2019). This kind of knowledge has been found to be a valuable source of information for further study: when the medicinal uses of 20 popular Cerrado plants were compared to their chemical compositions, results indicated a weak but significant correlation (Carvalho, 2004). Even urban locals tend to support the use of the Cerrado's medicinal plants. Two thirds of the people interviewed in one city in Minas Gerais would first appeal to medicinal plants in case of disease (Arnous et al., 2005).

7. Tropical Forests and Supporting Services

All the above-mentioned services depend on ecosystem functions, which in the ESs literature are considered "supporting services." According to the Brazilian ESs Law (Brasil, 2021), supporting services are "those that maintain the continuity of life on Earth, such as nutrient cycling, decomposition of waste, production, maintenance or renewal of soil fertility, pollination, seed dispersal, population control of potential pests and potential vectors for human disease, protection against solar ultraviolet radiation, and maintenance of biodiversity and

genetic heritage." Supporting services do not benefit people directly. Instead, they are the ecosystem functions that promote the other services (MEA, 2005).

In the literature, supporting services include, but are not limited to, nutrient cycling, habitat provisioning, primary productivity, and maintenance of biodiversity. In this review we highlight (a) the interactions between flora and fauna, such as pollination, seed dispersal, disease control, and (b) the interactions between the biotic and abiotic environments, involving nutrient-, water-, and light-related relationships. These latter interactions are used to better explain the maintenance of biodiversity and habitat provisioning services. All these relationships are detailed below.

7.1. Pollination

Pollination by animals is often necessary for plant reproductive success of both crops and native plants in natural vegetation areas; pollinators support genetic variability in plant populations and contribute to human food production and food security (Novais et al., 2016; P. E. Oliveira & Gibbs, 2000; Viana et al., 2012). Bees and beetles are the primary pollinators (Wolowski et al., 2019). They are associated with more than 90% of flowering plant species in tropical regions (Ollerton et al., 2011). Still, other insects, birds, and bats also play important roles as pollinators (Wolowski et al., 2019). In the Brazilian Cerrado, pollination services are provided predominantly by bees (32%) and other small insects (44%), but mammals (e.g., bats) and birds (e.g., hummingbirds) have important roles in tree and shrub pollination (Ishara & Maimoni-Rodella, 2011; P. E. Oliveira & Gibbs, 2000; Rabeling et al., 2019). The establishment and survival of bees depend on the availability of feeding and nesting resources, and species' degree of susceptibility to forest loss is related to their dietary specialization (P. A. Ferreira et al., 2015). Preserving natural forest areas near agricultural fields is vital to encourage pollinators' presence and support crop production.

Several studies have investigated the relationships between pollinators, forests, and croplands in the South American tropics, and many have attempted to quantify the value of the pollination services. For example, the value of bee pollination services provided by protected areas surrounding crops in a northern (Serra da Bocaina, state of Pará) and a southeastern Brazilian region (Mata do Jambreiro, state of Minas Gerais) was estimated at US \$564,000 years^{-1} and US \$246,000 years^{-1}, respectively (Hipólito et al., 2019). In palm oil plantations in the eastern Brazilian Amazon, the presence of forest reserves and riparian corridors contribute to the maintenance of orchid bees (*Apidae* and *Euglossini*), an essential group of endemic pollinators in the Neotropics (Brito et al., 2017). In cultivated areas in Ceará, Northeast Brazil, *Anacardium occidentale* (cashew) nut yield is directly correlated to flower visits by wild native pollinators, which were negatively affected by distance to a large forest remnant (Freitas et al., 2014). Protecting fragments of Atlantic rain forest was found to benefit pollination services there, providing gains for society that were both direct (US \$246,000 years^{-1}) and indirect (providing a large supply of pollen from up to 70 plant species) (De Marco & Coelho, 2004; Matos & Santos, 2019). When plantations are close to forests, pollination services may increase coffee fruit set by 28% (Saturni et al., 2016) and coffee productivity by 30% (Hipólito et al., 2019). Interestingly, pollination services by native bee and honeybee communities in coffee crops are differentially affected by landscape structure (Saturni et al., 2016): the abundance and richness of native bees were positively associated with forest cover and negatively associated with coffee cover; however, honeybee abundance was negatively associated with both forest and coffee cover. Pollination in the Cerrado is associated with a high diversity of flowering plants (P. E. Oliveira & Gibbs, 2000). The presence of natural or seminatural habitats in agricultural landscapes in the Cerrado increases the diversity and abundance of pollinators, resulting in an increase of at least 10% in crop productivity and improved quality of fruits, nuts, oils, and fibers (Klein et al., 2007). Pollination was estimated to contribute to 25% of soybean and cotton productivity, two of the main crops produced in the Cerrado (Giannini et al., 2015; Klein et al., 2007).

7.2. Seed Dispersal

Animal-mediated seed dispersal (zoochory) plays a meaningful role in Atlantic Forest regeneration and restoration, especially for woody and old-successional-stage species (Vespa et al., 2018; Viani et al., 2015). These species often exhibit specific fruit characteristics that are attractive to animals, such as fleshy fruit, pulp succulence, colorful exocarps, and large seeds (Martins, 2008). In highly fragmented landscapes, the presence of corridors affects the number and mobility of animals across the landscape, favoring forest regeneration (Bufalo

et al., 2016; Laurindo et al., 2019; Lourenço-de-Moraes et al., 2018). For *Euterpe edulis* (Juçara-palm), one of the species in high demand for supplying heart of palm (among other products), the loss of large frugivores such as migratory birds in remnant rain forests has led to a reduction in seed mean size, which may prejudice the regeneration of this and other trees (Galetti et al., 2013). In the Brazilian Cerrado, animals also perform an important function in forest regeneration and development through seed dispersal (Kuhlmann & Ribeiro, 2016). The prevalence of zoochory in the Brazilian Cerrado region increased from open physiognomies toward more diverse forest types, such as cerradão (savanna forest), where zoochory may reach 65% of the species pool (Gottsberger & Silberbauer-Gottsberger, 2018), thus strongly influencing the survival of trees and other woody species (Kuhlmann & Ribeiro, 2016).

7.3. Pest Control

The presence of forest fragments adjacent to agricultural systems increases landscape connectivity and preserves the sources of natural enemies of pests, such as birds and entomophagous insects (Boesing et al., 2017). On-farm pest suppression by birds is often higher in landscapes with higher native habitat cover and higher compositional heterogeneity, and when crop areas are closer to native habitats (Boesing et al., 2017). Native forest areas have a greater abundance of food resources and places for shelter for social and solitary wasps that feed on several agricultural pests. The highest abundance of such predatory wasps in the Brazilian Amazon is found at the edges of *Paullinia cupana* var. *sorbilis* (guarana) crops, near forest fragments (Somavilla et al., 2016). Social wasps are abundant and forage in soybean cultivation areas that are near remnants of native forest habitats (J. V. A. Ferreira et al., 2020). Although they feed on caterpillars present in both soybean and forest habitats, they often have perennial nests, and soybean cropped areas do not provide structure for nesting, which highlights the importance of forest preservation for biological pest control on crops (J. V. A. Ferreira et al., 2020). In the Atlantic Forest, the abundance and richness of different beneficial insect groups (i.e., wasps, bees, and flies) increase with natural forest area (Medeiros et al., 2019), contributing to decreasing incidence of pests in coffee crops (M. Q. Rezende et al., 2014). Similar dynamics were observed for predatory ants. In landscapes composed of coffee monocultures and containing at least 40% natural forest fragments, the presence of ants was found to reduce coffee berry borer incidence (Aristizábal & Metzger, 2019). Annual crops also benefit from the presence of forest fragments through increasing natural pest control, as observed in farms that grow tomatoes in the Brazilian Federal District. The control of *Bemisia tabaci* (whitefly) on 33 farms was greater on farms that had agroforestry integrated with vegetables (70.2%), compared with conventional farms (28.2%) (Togni et al., 2019). Forest and agroforest areas are important to natural pest enemies when abiotic conditions become more restrictive, such as during the Cerrado's dry season. They act as breeding sites and shelters, thereby maintaining the predator populations in the nearby farmland habitat (Harterreiten-Souza et al., 2021).

It is important to mention that the ecological integrity of tropical forests is essential for ensuring the diversity and abundance of plant-specialized pollinators, seed dispersers, and natural pest enemies. The health of these organisms depends on the availability of food, places of refuge, and nesting places provided by their natural habitats (Crall, 2019; Laurindo et al., 2019; Motta-Tavares et al., 2019; Viana et al., 2012). Beyond sustaining forests' capacity for self-maintenance and their ability to support life within the ecosystem, the provision of food, raw materials, and medicinal resources for human populations (Hagen et al., 2012; IPBES, 2016) supports life outside forests as well.

7.4. Disease Control

Forests are natural habitats for disease vectors and animal reservoirs that host pathogens. The distributions of these organisms depend on biotic and abiotic factors, such as temperature (Mordecai et al., 2019) and rainfall patterns (Dillon & Meentemeyer, 2019). In general, the transmission dynamics of infectious diseases, most notably vector-borne diseases, are commonly mediated by land-use changes that increase human contact with forest pathogens (Molyneux, 2008), such as malaria (De Oliveira Padilha et al., 2019). For example, a 10% increase in deforestation leads to a 3.3% increase in malaria incidence (MacDonald & Mordecai, 2019). However, this relationship is reciprocal: increased malaria occurrence is associated with roads, forest fires, and selective logging (Hahn et al., 2014), but a 1% increase in malaria leads to a 1.4% decrease in deforestation (MacDonald & Mordecai, 2019).

For waterborne diseases, the relationship between forests and disease incidence is more evident. For example, forest loss due to construction of dams and agricultural irrigation increases the prevalence of schistosomiasis

(Steinmann et al., 2006). As another example, disruption of hydrological services increases the risk of diarrhea in downstream communities (Pattanayak & Wendland, 2007), while increases in forest protected areas lower the incidence of diarrhea (Pienkowski et al., 2017).

Unlike infectious diseases that require a vector, which have a limited geographic distribution, noninfectious diseases can be spread farther by changes in climatic conditions, such as air quality, humidity, and temperature. In the Brazilian Amazon, during periods of intense fires, especially during extreme drought events, pollutants from biomass burning can increase cardiorespiratory morbidity and mortality rates (Jacobson, 2014; L. T. Smith et al., 2014) and induce genetic damage (de Oliveira Alves et al., 2017). In the Amazon Forest, the increasing occurrence of severe droughts has significantly increased the number of cases of respiratory diseases. During the 2005 drought, the total number of hospitalizations for respiratory diseases in children increased by between 1.3% and 180% in 77 municipalities (representing 31.3% of the municipalities affected by the drought), compared to the 10-year mean; in 2010, when another severe drought occurred in the region, this increase was between 1.2% and 267% in 197 municipalities (43% of the municipalities affected by the drought), also in comparison to the 10-year mean (L. T. Smith et al., 2014). On the other hand, the presence of undisturbed forests can help with disease prevention. The contribution of forests to climate cooling also provides a hospitable environment. Forests' cooling effects increase well-being and improve working conditions for many individuals. Even though mammals can acclimate to various heat conditions, they cannot dissipate their metabolic heat when the wet-bulb temperature exceeds a certain threshold (for humans: 35°C at 100% air humidity; or a higher temperature when humidity is lower) (Sherwood & Huber, 2010). By the end of this century, some locations in the Amazon may reach this temperature (Sherwood & Huber, 2010), and approximately 5 million people would be exposed to extreme heat stress for many hours, days, and months of the year (Hacon et al., 2019). Heat stress also has further consequences beyond health and well-being, such as lowering outdoor work feasibility, productivity, and economic health.

The conservation of natural tropical forests contributes to avoiding disease outbreaks (Keesing et al., 2006) by increasing biodiversity of vector and nonvector species, which, for example, increases competition for blood-feeding on vertebrates (especially mammals) and dilutes people's exposure to diseases throughout a more diverse pool of hosts (Laporta et al., 2013; S. S. Myers et al., 2013; Xavier et al., 2012). For instance, the effect of higher diversity leading to decreased risk of infectious disease (the “dilution effect”) occurs for hantavirus in the Atlantic Forest (Muylaert et al., 2019) and Chagas disease in the Amazon (Gottdenker et al., 2012; Xavier et al., 2012). Many disease outbreaks started in tropical regions: Africa with Ebola (Marí Saéz et al., 2015) and HIV (Rambaut et al., 2001); Australia with Hendra (Field et al., 2001); Asia with Nipah (Field et al., 2001) and MERS (Mohd et al., 2016); and South America with Machupo (Bradfute et al., 2011) and Chapare (Escalera-Antezana et al., 2020). The Amazon Forest is home to many species considered to have a higher chance of producing spillover events (i.e., disease transmission to humans), such as mammals from the orders Chiroptera, Primates, and Rodentia; it is also a region with relatively high potential for the discovery of new zoonotic diseases (Olival et al., 2017). Given the building anthropogenic pressure on Amazon natural systems associated with land use, it is possible that zoonotic spillover events will be occurring more often in the region.

At the time of writing, we are currently experiencing something that is probably the result of anthropogenic pressure on natural systems: the COVID-19 pandemic. The most widely accepted hypothesis for the origin of this disease is that a coronavirus (SARS-CoV-2) directly or indirectly spilled over from a mammal to humans (Wacharapluesadee et al., 2021). The pandemic's impact can be measured in human lives lost and in economic losses. The difference between the cost of prevention and the economic impact produced by the pandemic is astounding. By spending US $22.0–$31.2 billion yearly, deforestation in tropical forests and illegal wildlife trade could be significantly reduced, and preventive measures could be implemented to detect and avoid the next spillover event (Dobso et al., 2020). Most of this cost would be offset just by the value of the net carbon gain provided by keeping the forests standing (US $17.7–$26.9 billion) (Dobso et al., 2020). The difference between the economic impact caused by the pandemic (US$8.1–$15.8 trillion) (Dobso et al., 2020) and the costs to prevent such an event is striking. Furthermore, the economic impacts of ES losses and reductions extend far beyond this issue alone.

7.5. Maintenance of Biodiversity and Habitat Provisioning

Tropical forests—through their attributes of structure, composition, and function—provide the necessary mechanisms for their self-maintenance (C. W. Runyan et al., 2012, and references therein). This means that, despite

being very dynamic across temporal and spatial scales, tropical forests are systems in equilibrium (Salati & Vose, 1984). The maintenance of equilibrium is achieved through relationships between the fauna and flora (e.g., pollination, seed dispersal, and disease control) described above and the relationships between the biotic and abiotic components. The latter can be grouped into water-related, nutrient-related, and light-related interactions (Forrester & Bauhus, 2016). Light-related interactions deal with the role of the forest's structure in facilitating or controlling light entrance, absorption, and timing. Water-related interactions refer to the role of the biota in rainfall interception, plant transpiration, soil-water infiltration, and water storage, which are also known as ecohydrological processes. Nutrient-related interactions involve the nutrient cycling and uptake that maintain forest functioning and growth. Given the tropical regions' very poor and weathered soils, nutrient cycling through litterfall production and decomposition plays a fundamental role in maintaining vegetation structure and composition. All these processes refer to the provision of basic resources that maintain the ESs of tropical forests and the self-maintenance capacity of the ecosystems. And as discussed below, all three types of processes are highly interrelated.

7.5.1. Light-Related Processes

Light is one of the most important environmental factors for maintaining the survival and growth of tropical forests, as it is the source of energy for photosynthesis. Tropical forest structure and light are closely linked (Brinkmann, 1971; Fotis et al., 2018). The dense, closed canopy of tropical forests intercepts more light than the canopy of more open forests, increasing forest productivity (Clark et al., 2013; Duarte et al., 2021; Guan et al., 2015; Morin, 2015). In addition to the direct relationship with forest productivity, the link between the forest canopy and light is related to other ecosystem processes (Fotis et al., 2018). The canopy density influences the temperature and humidity conditions under the canopy through the balance between latent and sensible heat (Law et al., 2001) and shading effects (Niinemets & Valladares, 2004). The high canopy density favors the maintenance of soil humidity, which is another fundamental environmental resource for forest maintenance and growth. On the other hand, gaps in the canopy allow light to reach the forest floor, promoting evaporation (Law et al., 2001) and decomposing dead organic matter, directly affecting nutrient availability. These gaps also allow the establishment of pioneer species, which demand more light, in the understory (Oliver & Larson, 1996). The establishment of new species in the community can figure as an important factor in forest resilience to disturbances, such as, for example, landslides in forested areas that abruptly change the soil cover condition. Thus, through the control of light incidence, tropical forests control several processes fundamental for their own maintenance and survival (Brinkmann, 1971; Fotis et al., 2018) and, consequently, for ESs provisioning.

7.5.2. Water-Related Processes

Once established, the forest canopy promotes shading, which helps maintain moist conditions under the canopy. Many processes favor soil moisture in forest environments: (a) reduced evaporation through canopy shading (D'Odorico et al., 2007; Zeng et al., 2004); (b) increased infiltration of water into the soil, favored by the presence of understory and litter that reduces the energy of the rainfall and contributes to decreasing runoff and increasing infiltration (Boeken & Orenstein, 2001); and (c) the roots acting as a kind of funnel to drive rain water into the soil profile (Beven & Germann, 2013; Bush, 2017; Fattet et al., 2011; Ghestem et al., 2011; Joffre & Rambal, 1988). In addition to its role in climate and water regulation (Section 4), maintaining humid conditions throughout the year, even during dry periods, is an important mechanism for forest self-maintenance.

7.5.3. Nutrient-Related Processes

Tropical forests and nutrient cycles have strong reciprocal effects (Sanchez et al., 1985). Particularly important nutrient-related relationships of tropical forests involve the role of the forests in providing the nutrients necessary for their own maintenance and growth. Due to the elevated annual precipitation rates and high availability of solar radiation, soils of South American tropical rain forests and savannas are mostly poor in nutrients but highly variable in structure, texture, and water drainage capacity (Condit et al., 2013; Haridasan, 2008; Quesada et al., 2010, 2011). The growth of tropical forests in highly weathered soils is often supported by the feedback between vegetation and soils, mediated by climatic conditions (Caliman et al., 2020; Haridasan, 2008). The humid forests' warm and wet tropical climate favors litter decomposition and the release of nutrients, which are quickly absorbed by the forest (Luizao et al., 2004; S. Sellers & Bilsborrow, 2019). It has been shown that the deposition of nitrogen and phosphorus from litterfall and leaf litter decomposition partially compensates for the low content of these nutrients in soils (Caliman et al., 2020), helping organisms establish even within inhospitable environments

(Erwin et al., 2013). The interception of water by the canopy is an additional source of nutrients for plants. In addition, biotic components of these ecosystems, such as micro decomposers, macrofauna, and the vegetation itself (e.g., roots and litterfall), are key in regulating the soil's chemical, physical, and biological properties (Lange et al., 2015). The heterogeneity of the soils gives rise to different conditions of water availability and light incidence, thus providing habitats for a large and diverse biota.

Given the large spatial and temporal variability of these resources (i.e., light, water, and nutrients), the tropical humid and subhumid forests developed a diversity of characteristics—that is, plant functional traits—that help different species to survive in different forest habitats. For example, the ability of many plants to live in dystrophic and acidic soils in the Brazilian Cerrado is aided by certain functional traits, such as the ability to accumulate aluminum in leaves and other plant tissues or to exude organic compounds (Haridasan, 2008). Similarly, Cerrado species' investments in certain leaf traits, such as thick leaves and low nutrient accumulation in leaves, are considered evolutionary responses to nutrient-impoverished soils (Miatto & Batalha, 2016) and a long dry season (Sobral-Souza et al., 2015). Also, the low nutrient (e.g., assimilable nitrogen) and high aluminum content in Cerrado soils have been considered selective factors responsible for twisted trunks and branches (scleromorphism) (Arens, 1958). Habitat heterogeneity and plant functional traits are no doubt major forces influencing the maintenance of the great number of different organisms in tropical forests by offering a variety of suitable sites (refuges) in the landscape, reducing competition pressures among species that share common resources like light, water, and food (Ricklefs, 1977). They have also been considered important factors in supporting the resilience of forests to disturbances, such as small fluctuations in climatic conditions.

From the point of view of ecosystem stability, the self-maintenance capacity of the forests is considered a positive feedback, that is, more forest feeds more forest (Runyan & D'Odorico, 2014; Runyan et al., 2012). However, as seen below (Section 8), external drivers or internal imbalances can alter this web of functions, promoting a change in the ecosystem's regime (Scheffer & Carpenter, 2003; Scheffer et al., 2001). If a given system has at least two possible stable equilibrium states, instead of gradual changes, an abrupt change for a second equilibrium state might occur (Scheffer & Carpenter, 2003; Scheffer et al., 2001). It has been shown that, mainly under water-related constraints, tropical forests can jump to another stable state, which can be a grassland, another vegetation type (such as, e.g., a savanna), or bare soil (D'Odorico et al., 2007; Runyan & D'Odorico, 2014; Runyan et al., 2012). It has been shown that, despite the ability of tropical forests to maintain themselves through many biotic and abiotic interactions as described earlier, grasslands, once established, tend to be more stable than forests. That is because rebuilding a grassland after entering a bare state (arising e.g., because of a severe drought or a prolonged dry period) is more easy than the recovery of forests after such drivers (Forrester & Bauhus, 2016). Factors that affect the stability of ecosystems are also called drivers of change. The main drivers of change in humid and subhumid tropical forests are described in a following section.

8. The Role of Biodiversity in Providing ESs

While it is widely recognized that high biodiversity is a major driving force in creating ecosystem functions and functioning (Balvanera et al., 2006, 2018; Gamfeldt et al., 2013; Hooper et al., 2005; IPBES, 2019b; Isbell et al., 2011; Liang et al., 2016; Mori et al., 2017) the relationship between biodiversity and ESs is not entirely straightforward (Brockerhoff et al., 2017; Elmqvist et al., 2012; Mori et al., 2017). Some studies have reported a positive effect of species richness and functional diversity on ecosystem functions such as soil carbon storage, primary productivity, and microorganism-mediated decomposition (Hooper et al., 2005; Lange et al., 2015; Loreau et al., 2001); however the same relationship has not been found for the regulating services, such as erosion control and water quality improvement.

According to Lefcheck et al. (2015), one of the reasons biodiversity has not been recognized as equally important for each type of ES is because experiments, and the synthesis work derived from them, have focused on the effect of species richness only on a given function. Through a systematic review, they observed that the number of ecosystem functions directly increases with biodiversity. Thus, in addition to species richness, the multifunctionality of biodiverse ecosystems must be considered in the provision of ESs. Here, we argue that another factor affecting the difficulty of establishing a correlation between biodiversity and ESs relates to the proper definition of biodiversity.

The expression "biological diversity" has been used since the 1980s and, initially, referred only to the number of species that lived in a given region—that is, to the number of animals, plants and microorganisms in an area.

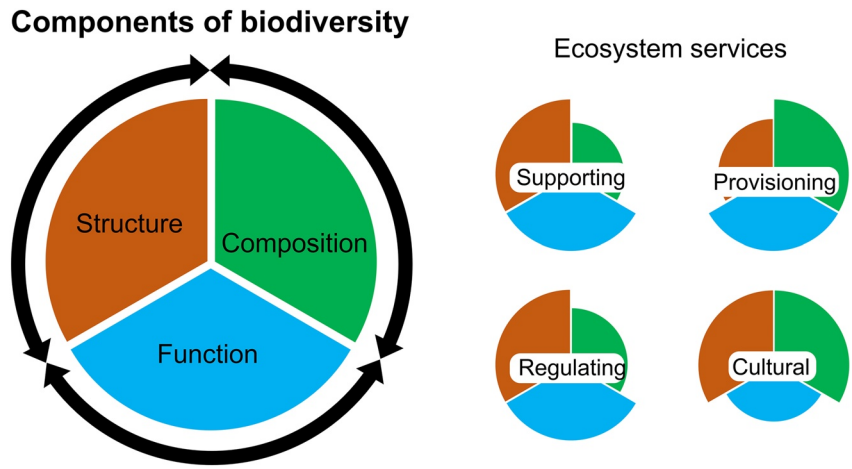

Figure 4. Components of biodiversity (structure, composition, and function) and their relative roles in ecosystem services.

Its meaning became more complex over time, also including other aspects of diversity, such as genetic diversity among organisms and diversity of traits and functions. In 1986, the entomologist Edward Wilson used the term "biodiversity" in place of the aforementioned expression (Wilson, 1994). Today, according to the Parties to the Convention on Biological Diversity, biodiversity is defined as the "*variability among living organisms from all sources, inter alia, terrestrial, marine, and other aquatic environments and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems*" (Höft, 2008). Despite being more comprehensive than the former definition of biological diversity, the biodiversity definition from the Convention on Biological Diversity still fails to capture the dynamics and the wide range of functions that comprise biodiversity (Mace et al., 2012).

With respect to ESs, most existing definitions of biodiversity are not as helpful as they could be, because they are somewhat vague and do not convey the importance of biodiversity for ecosystem functioning and functions (Mace et al., 2012; Noss, 1990); these definitions result in a common misconception that reduces biodiversity to a synonym of species richness. According to Noss (1990), we should instead focus on the attributes of biodiversity—that is, structure, composition, and functions (Franklin et al., 1981; Lamont, 1995; Noss, 1990)—and their role in supplying ESs. Composition has to do with the variety of elements at various levels of an ecosystem, including genetic diversity and diversity of species, populations, and traits; it also includes diversity of ecosystems, communities, and landscapes. Structure is the physical organization at various levels, including genetic structure, population structure, community physiognomy and habitat structure, and landscape patterns. Functions comprise the above-described ecosystem functions that occur via energy and matter transfers, involving biotic-abiotic interactions (e.g., soil fertilization and nutrient cycling) and biotic-biotic ones, such as pollination and seed dispersal by animals (zoochory) among many others. As shown in Figure 4, these attributes are not independent entities, but strongly interact with each other (Lamont, 1995). Thinking in terms of biodiversity attributes makes it easier to understand the important role that all these attributes play in supplying ESs (Figure 4).

To highlight the role of the biodiversity in the studied ESs, in Table 5 we summarize the main ES types for each biome studied. Based on the ESs as discussed in Sections 4–7 and on the data presented in Table 5, we can see that regulating and supporting services are more strongly correlated with structure and functions, and less strongly with composition; provisioning services are more strongly related to composition and functions, but less related to structure; cultural services are more strongly related to structure and composition, but less related to functions. Considering that these attributes are all intrinsic to the biodiversity, we can say that, in essence, biodiversity does play a role in all of the ESs (Table 5, Figure 4).

It is important to mention that a review carried out by Van der Hoff et al. (2022) points out the strong tendency of studies that address ESs in South America to focus on greenhouse gases, especially carbon. This trend is probably related to the challenges of measuring the elements and processes that characterize other types of ESs—for example, those related to biodiversity and culture—which still do not have clear methods; this makes it difficult to assess and incorporate them into public policies (van der Hoff et al., 2022). In addition, understanding the value

Table 5
Ecosystem Services and Relationships With the Biodiversity Attributes: Structure, Composition, and Function

Biome	Biodiversity attribute	Ecosystem services	References
		Regulation services	
Amazon Forest	Forest cover	Thermal regulation	Culf et al. (1996)
	Forest volatile organic compounds (VOCs) emission and diversity	Rainfall recycling	Pohlker et al. (2012), Poschl et al. (2010), and Malhi et al. (2021)
	Vegetation cover and canopy conductance	Water regulation	M. H. Costa and Foley (1997)
	Tree functional diversity	Natural disaster regulation; extreme drought dampening	Nepstad et al. (1994), Brum et al. (2019), and Barros et al. (2019)
Atlantic Forest	Forest continuity	Thermal regulation	Ewers and Banks-Leite (2013) and Wanderley and Miguel (2019)
	Forest cover	Natural disaster regulation	Campos et al. (2021)
	Forest cover and structure	Water quality and erosion control	Avanzi et al. (2013)
Brazilian Cerrado	Vegetation cover type, tree density, root distribution, and litterfall	Water regulation	R. S. Oliveira et al. (2005), Rosalem et al. (2018), Borma et al. (2009), da Rocha, Manzi, Cabral, et al. (2009), Mendes et al. (2019), and Hunke et al. (2015)
	Forest cover and structure	Water quality and erosion control	Guerra et al. (2014), Anache et al. (2017), Hunke et al. (2015), and Falcãodo et al. (2020)
		Provisioning services	
Amazon Forest	Population abundance of hunted species; and seasonal fluctuation in consumed species	Wild food provision	Shanley and Medina (2005), Tonini and Pedrozo (2014), Homma et al. (2006), A. L. da Silva & Begossi (2009), Adams et al. (2005), De Souza-Mazurek et al. (2000), and Antunes et al. (2019)
	Medicinal-plant composition	Provision of medicinal products	Pennaforte (2003), C. D. B. Ribeiro et al. (2021), A. P. Mendonça and Ferraz (2007), and C. N. Dias et al. (2015)
Atlantic Forest	Edible-plant composition and genetic variability	Wild food provision	Christo et al. (2012), Joly et al. (2014), and Quinteiro et al. (2015)
	Medicinal-plant composition	Provision of medicinal products	V. B. Oliveira et al. (2012) and Dutra et al. (2016)
Brazilian Cerrado	Medicinal-plant composition	Provision of medicinal products	Guarim-Neto & de Morais (2003), de Mendonça et al. (1998), De Castro Peixoto et al. (2019), Luiz-Ferreira et al. (2010), Mousinho et al. (2011), and C. D. B. Ribeiro et al. (2021)
	Edible-plant composition and genetic variability	Wild food provision	Pereira et al. (2012), Sousa Júnior et al. (2013), and E. A. Vieira et al. (2008)
		Cultural services	
Amazon Forest	Forest structure, composition, and functioning	Cultural identity and traditional knowledge	Barbosa and Moret (2016), T. P. da Silva et al. (2020), and Homma (2014)
Atlantic Forest	Forest structure, composition, and functioning	Cultural identity and traditional knowledge	Conde et al. (2017), De Souza et al. (2018), de Santana et al. (2016), and de Oliveira (2007)
Cerrado	Forest structure, composition, and functioning	Cultural identity and traditional knowledge	Carvalho (2004) and Anderson and Posey (1985)
		Supporting services	
Amazon Forest	Forest cover (%) and connectivity	Disease control	MacDonald and Mordecai (2019)
	Forest connectivity	Genetic resources	Aleixo et al. (2019) and Ribas and Aleixo (2019)
	Species richness, composition, and forest cover and connectivity	Pollination	Brito et al. (2017)
Atlantic Forest	Forest cover and connectivity	Pest regulation	Aristizábal and Metzger (2019) and Boesing et al. (2017, 2018)
	Species and habitat diversity	Disease control	Muylaert et al. (2019)

Table 5
Continued

Biome	Biodiversity attribute	Ecosystem services	References
	Woody species richness and dominance	Productivity	Rodrigues et al. (2019)
	Tree basal area and height	Soil fertility	Mendes et al. (2019)
	Forest connectivity	Pollination	Freitas et al. (2014)
Brazilian Cerrado	Species richness and spatial dissimilarity	Habitat provisioning	Camargo et al. (2018) and Carmignotto et al. (2022)

of biodiversity and cultural services for local and non-local people demands stronger interactions with the people and their communities.

8.1. Biodiversity, Ecosystem Shifts, and Ecosystem Resilience

Anthropogenic disturbances such as deforestation, climate change, severe droughts, fire, habitat fragmentation, harvest, or reduction of species diversity can promote significant changes in ecosystems, acting as drivers of change (Sections 9 and 10). Depending on the system and the type of disturbance—including the potential occurrence of synergistic effects between the drivers—these changes, instead of occurring smoothly and continuously (Tilman, 2001; Vitousek et al., 1997), may occur in abrupt and sometimes unexpected ways (Beisner et al., 2003; Folke et al., 2004; Ludwig et al., 1997; Scheffer & Carpenter, 2003; Scheffer et al., 2001). When the system's resilience can no longer absorb the impacts, a tipping point is reached (Lenton et al., 2009). After the tipping point, the system jumps to another equilibrium state. For forested ecosystems, this second state can be bare soil, grassland, or even a different type of vegetation, such as, for example, an impoverished savanna (Lovejoy & Nobre, 2018; Nobre & Borma, 2009; Nobre et al., 1991).

If external drivers are able to induce an ecosystem to turn into another state, it means that the system has two (or more) *alternative equilibrium states* (i.e., alternative stable states) (Figure 5). The movement from one state to another is known as a *regime shift* (Scheffer & Carpenter, 2003). The point at which the system change from an equilibrium state to another represents the *tipping point* of the system, that is, the threshold at which the regime shift takes place (represented by the point V1 in Figure 5). A system's resistance to moving from one equilibrium state to another is called *resilience*, while the difficulty in returning to the initial state is called *hysteresis*. Hysteresis means that the simple reversion of the drivers to conditions present before the abrupt change is not enough

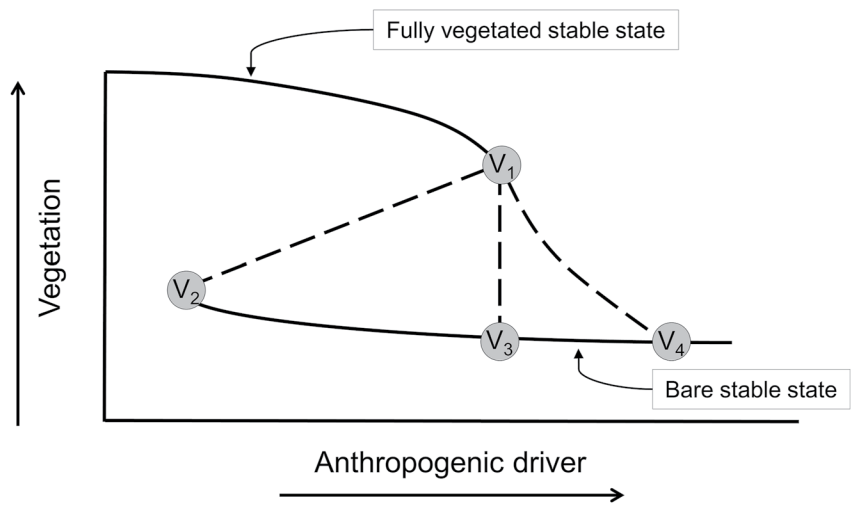

Figure 5. Conceptual illustration of regime shifts and the occurrence of two stable states: a fully vegetated stable state and a bare state stable. V1 represents the tipping point. If the threshold is surpassed, the system is pushed toward the alternative vegetation state (i.e., bare state). The bare state side can be achieved if the anthropogenic drivers increase (V4), maintain (V3), or even decrease (V2). After reaching V2, V3, or V4, it is easier for the system to maintain the bare state than to return to the vegetated state (V1). The resistance of the ecosystem against reaching V2, V3, or V4 is called resilience (adapted from Runyan et al. (2012)).

to return the system to the previous condition (Holling, 2013; Scheffer & Carpenter, 2003; Scheffer et al., 2001). The potential occurrence of regime shifts has been documented for a number of other ecosystems (see Thresholds Database on the Web site http://www.resalliance.org), along with significant losses of environmental services and great losses for human societies (Gunderson & Holling, 2002; Runyan et al., 2012, 2015).

The potential occurrence of gradual or abrupt shifts in a given ecosystem depends on the magnitude of the driver of change and on the resilience (Folke et al., 2004). Biodiversity has long been linked to ecosystem resilience and to the ability of ecosystems to withstand the actions of external agents while maintaining basic ecosystem functions (Andresen et al., 2018; Emmett Duffy, 2009; Loreau et al., 2001; Mace et al., 2012; Thompson et al., 2012). This capacity is fundamental in times when global changes are becoming faster and more intense (IPCC, 2021). However, it is known that anthropogenic actions now have the potential to damage biodiversity at unprecedented levels (Arroyo-Rodríguez, Saldaña-Vázquez et al., 2017; Newbold et al., 2015; Van Der Plas et al., 2016). In addition, the combined effects of climate change and biodiversity loss are highly uncertain and have the potential to push the Earth system into another equilibrium state (Lenton, 2011; Lenton et al., 2009), with severe impacts on natural environments, global economy (Runyan et al., 2015), and consequently, human well-being (Gunderson & Holling, 2002).

With these possibilities in mind, in the study of the ESs provided by tropical forests, it is important to identify ecosystems at risk of suffering abrupt changes to an alternative stable state. In the humid and subhumid tropical forests studied here, we can cite the Amazon Forest (Hirota et al., 2021; Lovejoy & Nobre, 2018; Nobre & Borma, 2009), the Atlantic Forest's cloud forests (Bruijnzeel, Kappelle, et al., 2011), and the seasonally flooded forest of the Amazon (Flores, 2016; Flores et al., 2016, 2019) as systems with potential to suffer abrupt changes and regime shifts towards a less vegetated state (or an abrupt change in the dominant vegetation type). In Section 9, we discuss the potential shifts of the Amazon to a savanna state—that is, the savannization hypothesis (Nobre et al., 1991)—and the potential mechanisms of forest resilience. We will also discuss the impacts of the ecosystem shift in the ESs provided by the Amazon Forest if an abrupt shift occurs.

9. Land Cover Changes in South American Tropical Forests and Impacts on ESs and Economy

9.1. Deforestation

Despite their large biodiversity and recognized importance in terms of ESs provisioning, tropical countries have the highest global rates of forest loss. Monitoring of tropical forests reveals that South America is historically the region with the highest area of deforestation. Between 2000 and 2010 the annual average rates reached 5×10^6 ha yr^{-1} for the continent. This rate fell by around 50% between 2010 and 2020, but even so, forest loss on the continent remains among the highest in the world (A. Salazar et al., 2015). Deforestation is particularly intense in three South American biomes: the Tropical Savannas (which lost 1,326,348 km^2 from the Brazilian Cerrado and the Venezuelan Chaco), the Atlantic Forest (which lost 978,031 km^2), and the Amazon Forest (which lost 918,473 km^2) (A. Salazar et al., 2015). Brazil, in particular, plays a key role in the dynamics of tropical forests. The country is home to 12% of total global forests (Global Forest Watch, 2020; https://www.globalforestwatch.org/) and holds most of the area of the Amazon Forest, South American Tropical Savanna, and Atlantic Forest biomes. Across the entire Amazon biome, it is estimated that more than 62% of all deforestation that occurred between 1985 and 2020 occurred in Brazil (MapBiomas, 2020; Souza et al., 2020).

It is estimated that the whole Amazon biome has already lost 17% of its original forest (RAISG, 2020), putting biodiversity and the regional and global climate balance at risk. Even when the Amazon forest experienced a reduction in its deforestation rates (2004–2012), it was subjected to intense forest degradation, with the degraded area covering more than twice the deforested area (Matricardi et al., 2020). It is estimated that around 17% of forest mapped between 1995 and 2017 in the Amazon biome is experiencing some level of forest degradation (Bullock, Woodcock, & Olofsson, 2020; Bullock, Woodcock, Souza, et al., 2020). High rates of deforestation also have been registered for the Tropical Savannas. The Brazilian Cerrado and Dry Chaco biomes are currently considered the most active agricultural frontiers in South America (Baldi et al., 2015; Le Polain de Waroux et al., 2018; M. O. Pires, 2020). Of the total area deforested in the South American Tropical Savannas (1,326,348 km^2), around 79.6% is in the Brazilian Cerrado (1,056,038 km^2). The total area lost in the Brazilian Cerrado is larger than the total deforested area of the Amazon and Atlantic Forests (Salazar et al., 2015). In Brazil, the area of original vegetation remaining in the Brazilian Cerrado does not exceed 50% (A. Salazar et al., 2015; R. R. S. Vieira

et al., 2018). The effects of deforestation in the Brazilian Cerrado are aggravated by the increased fragmentation of forest remnants and the growing loss of connectivity, which directly affects ecosystem functioning and services (Grande et al., 2020).

The Atlantic Forest is the Brazilian biome with the highest level of human occupation. Different estimates suggest that the remaining area of primary forest in the biome is from 11% to 26% of its original size (Fundação SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais, 2018; M. C. Ribeiro et al., 2009, 2011). Intensive urbanization and agricultural expansion in the biome have reduced forests to island-like fragments, generally of <50 ha, vulnerable to degradation and its effects, such as changes in ecological relationships, edge effects, and changes in the microclimate (Arroyo-Rodríguez, Melo, et al., 2017; Arroyo-Rodríguez, Saldaña-Vázquez, et al., 2017). A sizable portion of the forest remnants (20%–40%) are concentrated in high-altitude and sloped areas. Hilltops and areas with slopes greater than 45° are legally protected by the Brazilian Forest Code (Law 12651, Brasil, 2012). Compared with the Cerrado and Amazon biomes, the current rate of deforestation in the Atlantic Forest is significantly lower. However, its forest remnants are becoming increasingly fragmented, especially those smaller than 10 ha (Bicudo da Silva et al., 2020; Santos et al., 2018). Considering its low percentage of remaining forest and the high level of fragmentation, further deforestation of the Atlantic Forest biome could jeopardize the capacity of its forests to provide ESs in the short term (Bittencourt et al., 2020; Sansevero et al., 2020).

According to analysis carried out by Souza et al. (2020), the Atlantic Forest lost ca. 99,000 km^2 between 1985 and 2020, although the area of forest has increased since 2004. Although the Brazilian Forest Code plays an essential role in forest conservation in the region, especially in Permanent Preservation areas, the same law requires that private properties in the Atlantic Forest maintain a minimum forest area of 20%. This level of protection is considered deficient owing to the state of the forest remnants, the region's ecological importance, and the pressures of land use dynamics in the biome. In addition, only 4.7% of Brazil's public Conservation Units are in the Atlantic Forest biome, occupying 1,201,220 km^2, which is equivalent to only 9% of the biome. Protected areas in the biome represent only 30% of the remaining forest (C. L. Rezende et al., 2018). Several programs have been implemented for recovering the Atlantic Forest, which may be part of the reason for the observed drop in deforestation rates since 2004 (A. Salazar et al., 2015).

Although practices may differ in response to policies and economic and socio-environmental constraints, the main drivers of deforestation are similar in these three biomes and their subregions: deforestation is directly triggered by the expansion of the agricultural frontier, illegal mining, and development of infrastructure such as highways and hydroelectric plants—and indirectly by political and economic dynamics (Armenteras et al., 2019; Carrero et al., 2020; Hecht & Rajão, 2020).

9.2. Impacts of Forest Loss on Soil Fertility and Water Quality

Erosion is an environmental, social, and economic problem in South America (Ananda & Herath, 2003; Hugo, 2008; Santibáñez & Santibáñez, 2007). It is estimated that about 75 billion tons of soil are eroded from the world's terrestrial ecosystems each year (Pimentel & Kounang, 1998) due to modified human activities. The rates of soil loss in Brazil exceed 50 t ha^{-1} yr^{-1} (Guerra et al., 2014). In South America, deforestation is associated with extensive cattle ranching, and from a degraded land of 100 million ha, animal grazing have considered to be responsible for 70 million ha land degradation (Hugo, 2008). Deforestation and forest degradation reduce or eliminate the canopy and the understory, exposing the ground to the intensity of radiation and torrential rains and creating an open window for erosion (Flores et al., 2019). Although the amount of soil loss in a single rainstorm is almost unnoticed, when scaled to hectares of cropland, the loss can exceed 15 tons (Pimentel & Kounang, 1998). When a terrestrial ecosystem is repeatedly disturbed, the interaction between the remaining sparse vegetation and high soil erosion rates may reshape the stability of natural tropical forests to a permanent state of degraded savanna (Flores et al., 2019). See also Section 9.

Different authors have characterized the adverse effects of soil erosion for both “on-site” and “off-site” landscapes (Bennett, 1935; Pimentel et al., 1995). The impacts of the erosion for on-site landscapes are losses of soil, nutrients, and organic matter; reductions in the soil's chemical, physical, and biological fertility; yield drops; production losses; and shrinkage of the available planting area. The research recommends reforestation or mulches that will act as a forest soil litter cover protecting soil against erosion and application of conservation techniques to improve the soil's physical properties, especially in terms of reducing compaction (Jordán et al., 2010; Nzeyimana et al., 2017).

The off-site landscape impacts of erosion largely relate to compromised water quality (Fernández-Raga et al., 2017). Excess nutrients and sediments in water bodies may compromise the dissolved oxygen levels and light penetration, which are fundamental for organisms living and growing and for the quality of the water bodies. Major off-site problems include earth-dam failures, eutrophication of waterways, siltation of harbors and channels, loss of reservoir storage, loss of wildlife habitat, disruption of stream ecology, increase in the risk of natural disasters (landslides and debris flow), and increasing costs of water treatment (Gray & Leiser, 1989).

9.3. Impacts of Land Use and Land Cover Change on the Economy

Over the last three decades, a growing number of studies have attempted to estimate the value of the ESs provided by forests beyond carbon maintenance and sequestration. Yet methodological approaches and resultant values widely differ. In South American tropical forests, the value of ESs may have decreased by US $81.65 billion due to cropland expansion between 1992 and 2015 (Li et al., 2019). This represents nearly half of the total value reduction due to cropland expansion in all tropical forests (i.e., US $166.83 billion), which held about 1.17% of the value of terrestrial ESs value in 1992—the equivalent of US $14.7 trillion (Li et al., 2019). Using value aggregations (i.e., benefits transfer), different studies have arrived at other estimates. For example, estimates of the average marginal value of the Brazilian Amazon ranged between US $431 and US $3,135 ha^{-1} yr^{-1} in the 1990s (Andersen et al., 2002; Torras, 2000), while estimates of the marginal value for tropical forests worldwide were over US $5,000 ha^{-1} yr^{-1} in the first decade of the twenty-first century (Costanza et al., 2014).

A spatially explicit valuation study of four types of ESs in the Brazilian Amazon (food production, provision of raw materials, climate regulation, and greenhouse gas regulation) shows that their combined marginal value may reach up to US $737 ± 134 per hectare per year (Strand et al., 2018). Another study has estimated that European households would be willing to pay US $8.4 billion per year for avoiding forest losses in the Amazon in 2050 (Navrud & Strand, 2018). Despite the differences in scientific approaches to ESs valuation, the central premise of these studies is that ESs provide valuable benefits to society and evaluation of these services demands a spatially and temporally explicit perspective that can show the relationships between beneficiaries and ESs provision (Fisher et al., 2011). This approach could also reveal how different social groups may emphasize the importance of specific ESs (Caballero-Serrano et al., 2017).

Valuation studies look at how diminishing or sustained ESs provision might affect agriculture economically. For example, the production of soy and beef in some Brazilian regions may lose up to US $9 ha^{-1} yr^{-1} from declining productivity due to reduced rainfall (Strand et al., 2018); rainfall is a well-recognized ES provided by tropical forests (Section 5). Double-cropping systems (mainly soybean/cotton and soybean/maize) may also be jeopardized, as they are highly dependent on spatial patterns of rainfall (Arvor et al., 2014) and on rainfall before and at the beginning of the wet season (Spangler et al., 2017). Systems in the Amazon-Cerrado transition region may experience a 17% decrease in agricultural productivity by 2050, while in the northern Brazilian Cerrado, a region called MATOPIBA—an acronym for the states of Maranhão, Tocantins, Piauí, and Bahia—may see productivity losses reaching up to 61% (Abrahão & Costa, 2018), thereby threatening double-cropping sustainability (G. F. Pires et al., 2016). There is already evidence that large-scale deforestation is causing substantial economic losses. For instance, Leite-Filho et al. (2020) show that due to current deforestation patterns, the duration of the rainy season in the southern Amazon has already been reduced by a month, on average, leading to an increased risk of losses of the second crop in the region (see Section 4.2.4).

Economic impacts are not restricted to the agricultural sector. Logging may decrease productivity by US $39 ± 30 ha^{-1} yr^{-1} due to invasive fire occurrences (A. S. Oliveira et al., 2019), and the likelihood of such losses is higher as forest fires become more frequent (Barlow et al., 2019). The Xingu, Tapajós, and Madeira basins (southern and southeastern Amazon) have high hydropower potential, but power generation at the end of the dry season could be jeopardized due to late onset of the rainy season (Arias et al., 2020; Sumila et al., 2017). Moreover, the delayed onset may jeopardize water provision to the water reservoirs during the most critical period (i.e., after the dry season), such as occurred during the 2013–2015 drought in São Paulo, which was partially due to low precipitation levels in some headwaters of the LPB during the dry to wet transition (Milano et al., 2018).

10. The Future of the Amazon Forest: Drivers of Change and Forest Responses

The more we learn about the functioning of the Amazon and the countless ESs it provides, the more serious is our concern about the future of this rain forest, given the constant threats that hang over it. Besides the direct effects

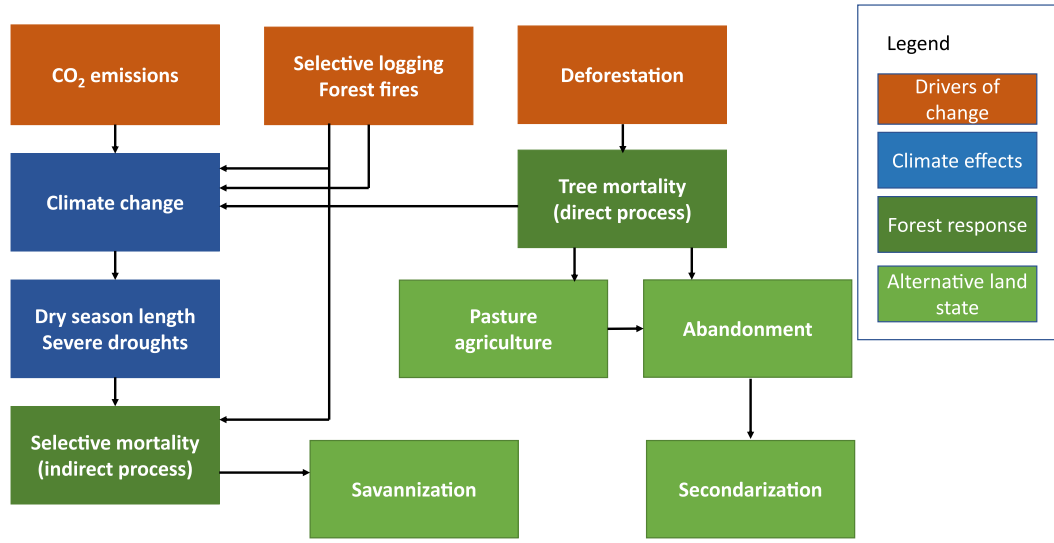

Figure 6. Anthropogenic drivers of changes and their effects on climate and forest responses.

of deforestation, selective logging, and fire, indirect impacts of climate change (through increases in atmospheric CO_2, temperatures, and severity of extreme events, as well as prolonging of the dry season) also threaten the composition, structure, functioning, and functions of the Amazon rain forest. The Amazon's high biodiversity plays a fundamental role in the rain forest's resilience to these impacts (see Section 8.3). However, there are limits to this resilience, which can be reached when the drivers of forest loss act synergistically, amplifying threats and inducing the system to achieve another equilibrium state. Therefore, understanding how the Amazon rain forest may respond to anthropogenic drivers of change is crucial for predicting its capacity to maintain ESs.

This section deals with the anthropogenic drivers of forest loss—namely global and regional climate change, deforestation and selective logging, fires, and prolonging of the dry period—and their synergistic effects on the functioning and stability of the Amazon Forest over different time scales (Figure 6). We specifically address the Amazonian savannization hypothesis, which suggests that the synergy among these drivers (i.e., positive feedback) may promote a profound change in the rain forest structure and composition when it hits a tipping point, transforming it from a humid forest to an impoverished savanna, dominated by species more tolerant to droughts and fires (Lovejoy & Nobre, 2018; Nobre & Borma, 2009; Nobre et al., 1991). Below we describe these drivers individually, followed by an analysis of the potential pathways of change—that is, the possible future of the Amazon Forest.

10.1. Drivers of Forest Loss and Potential Drivers of Ecosystem Shifts

As described in Section 8.1, until the 1970s, the 6.2 million km^2 occupied by the Amazon rain forest remained relatively intact. Then, due to the Brazilian government's plans to develop this region—plans known as Avança Brasil—deforestation rates rose. Incentives for the Amazon's development became synonymous with deforestation, since rain forest removal was accepted as evidence of land occupation, making companies eligible for government tax incentives (Lima, 2005). This happened from the 1970s to 1990s. After that, deforestation rates in the Amazon have been increasing annually, with interannual variations responding directly to the economic incentives, political constraints, and monitoring.

One could imagine deforestation occurs suddenly, beginning with intact forest and ending with the complete conversion of the rain forest into other land cover types. However, deforestation does not imply an immediate elimination of the forest. Instead, it is a dynamic process that happens in stages that may take years, during which rain forests are submitted to a succession of forest removals until the area becomes utterly degraded (INPE, 2008). The clear-cut is the final stage of the deforestation process. During this process, pastures can be an alternate use of the area, which may or may not later become agricultural areas, depending on economic drivers (e.g., trade in timber, livestock, and crops). When the deforested site no longer serves economic interests, it is abandoned and converted into secondary vegetation areas. The type of secondary vegetation it becomes—that is,

closed-canopy vegetation with mature forest species and high biodiversity or poor, open-canopy vegetation with light-demanding species (i.e., grasses)—will depend on land practices undertaken after the land abandonment. So, as the ultimate result of deforestation, rain forest areas can be transformed into pastures, agricultural areas, or simply degraded forests (Figure 6).

10.2. Selective Logging

Another human activity that directly impacts the Amazon is the land degradation associated with selective logging. Forest degradation decreases forest biomass and reduces forest capacity to provide ESs (Parrotta & Agnoletti, 2012). As areas degraded by selective logging do not necessarily coincide with the deforested areas, selective logging is a distinct form of land use and change in the Amazon (Asner et al., 2006). Between 1999 and 2002, logged areas ranged from ca. 12,000 to 20,000 km^2 per year (Asner et al., 2006). According to INPE (2008), 15,000 km^2 of rain forest was degraded by selective logging in 2007 and 25,000 km^2 in 2008. From 1998 to 2019, the Amazon forest experienced intense forest degradation, affecting an area more than twice the area deforested annually (Matricardi et al., 2020). It is estimated that between 1995 and 2017, forest degradation in the Amazon reached 366,300 km^2 (Bullock, Woodcock, & Olofsson, 2020; Bullock, Woodcock, Souza, et al., 2020).

10.3. Forest Fires

Under the natural conditions of high precipitation and high atmospheric moisture, the spontaneous occurrence of fire in the Amazon rain forest is relatively rare. However, deforestation and selective logging make the rain forest more vulnerable to dryness and flammability through the greater incidence of solar radiation, increases in the soil temperature, and supply of the flammable material (dry litter and soil) (Alencar et al., 2004; Aragão et al., 2007; Barlow & Peresa, 2004; Cochrane & Schulze, 1999; Laurance et al., 1998; Nepstad et al., 1999). In addition, rain forest areas located near the deforested areas are also more vulnerable to fire. Fire occurrence in the Amazon occurs close to road networks and in deforested neighborhoods where agricultural practices occur (Cochrane & Barber, 2009; M. F. Cardoso et al., 2003). Severe droughts and prolonged dry periods can also increase the incidence of fires (Aragão et al., 2007; M. F. Cardoso et al., 2009; Nepstad et al., 1999).

10.4. Global Climate Change

Global climate change results from increased CO_2 emissions from human activities such as fossil fuel burning. It has been shown that the elevated concentration of CO_2 in the atmosphere influences biogeochemical fluxes of water and energy between the rain forest and the atmosphere, increasing the global average air temperature and accelerating the global hydrological cycle, in response to an increase in the evaporation and transpiration rates. While an increase in the average air temperature through the greenhouse effect is more evident, the same is not true for rainfall, because rainfall rates may increase in some regions but decrease in others (IPCC, 2013). For the Amazon Forest region, it has been suggested that global climate changes could reduce rainfall, through an increase in the severity and length of the dry period (Gatti et al., 2021). These global effects may be amplified by local activities such as deforestation and selective logging, which directly affect the forest structure and composition, causing changes in the local and regional climate through biogeophysical processes (see Section 4.1).

10.5. Forest Responses to Anthropogenic Drivers of Change

All the above-mentioned anthropogenic drivers of change can influence the behavior and functionality of the rain forest directly or indirectly, via changes in the climate patterns. Since vegetation and climate are strongly coupled through biogeochemical and biogeophysical processes (Section 6), changes in the local climate as a result of global and local human activities will ultimately impact the rain forest functioning and provision of ESs. Some drivers, such as deforestation, selective logging, and fire, threaten the forest directly, through suppression and mortality. Other factors, normally related to climate responses to these changes—for example, increased temperature, decreased rainfall, and prolonged dry period—may indirectly affect vegetation, promoting selective mortality and changes in forest structure and composition (Figure 6). Changes in the forest structure can result in profound changes in the intrinsic characteristics of the biomes, directly affecting forest composition, functions, and resilience to abrupt changes. Below we present an overview of the rain forest's primary responses to anthropogenic drivers.

10.5.1. Forest Mortality

Forest mortality is a direct result of deforestation and selective logging. However, selective forest mortality can also be indirectly induced through severe droughts, fire, increased atmospheric concentrations of CO_2, increased air temperature, and a prolonged dry season (Figure 6).

Warmer air temperatures tend to reduce forest productivity rates (Sullivan et al., 2020), particularly by intensifying the atmospheric vapor pressure deficit (VPD; M. N. Smith et al., 2020). An increase in the temperature inside the forest (resulting from an increase in global temperature or due to an open forest structure that facilitates incidence of solar radiation) results in an increase in the VPD inside the forest (M. N. Smith et al., 2020). The greater the VPD, the greater the water demand from the atmosphere, and the faster the transpiration rate. These conditions can result in plant mortality due to hydraulic failure for species less resistant to drought or individuals with no access to soil water (Rowland et al., 2015).

It has been shown that plant mortality through changes in the climatic pattern is selective, and larger mortality rates are mainly associated with plant traits such as trunk size (Nepstad et al., 2007; Rowland et al., 2015), plant growth rate (Esquivel-Muelbert et al., 2020; Phillips et al., 2010), and lower wood density (Coelho de Souza et al., 2019). It has been shown that the larger and taller trees are more vulnerable to droughts (Giardina et al., 2018) and have higher mortality rates during severe droughts (Esquivel-Muelbert et al., 2020; Nepstad et al., 2007; Phillips et al., 2009). The mortality of larger trees has an important implication for the survival of the forest. These trees store more carbon, and when they die, they emit more CO_2 into the atmosphere. These are also the trees with higher transpiration rates because of their greater active xylem area (Kunert et al., 2017). Their mortality leads to the suppression of a critical fraction of ET from the forest, which can impact the processes of rainfall recycling (Kunert et al., 2017). It is important to note that the drought-induced mortality of larger trees challenges our understanding of one of the important forest resilience factors to droughts, which is the absorption of water by deep roots (Nepstad et al., 2004).

But it is not only droughts that increase forest mortality. Water in excess is also a potential cause of tree mortality (Aleixo et al., 2019). Esquivel-Muelbert et al. (2020) observed that drought-tolerant species were at great risk of death in the east-central Amazon due to an excess of water.

The increase in CO_2 concentrations in the atmosphere due to global climate change was, at first, considered to be a negative feedback from climate change, given that it favors photosynthesis and, therefore, faster vegetation growth, in a process known as CO_2 fertilization (Norby et al., 2005). However, faster growth has also been associated with early mortality (Bugmann & Bigler, 2011). The observed increase in the mortality rate of the Amazon rain forest since the mid-2000s was associated with high climate variability and the trade-off between accelerated growth and early mortality (Brienen et al., 2015). Selective mortality in fast-growing species was also observed in a 30-year survey in the Amazon rain forest (Esquivel-Muelbert et al., 2020).

Tree mortality results in a forest condition similar to that resulting from the selective logging effect; that is, clearings are opened in the forest, allowing the entrance of solar radiation and wind in the open canopy. These conditions favor dryness and, consequently, higher transpiration rates and fire occurrence, thus creating a positive feedback for forest degradation and climate change.

10.5.2. Transition to Secondary Forest

When a deforested area is abandoned, which is not uncommon in the Amazon (Nanni et al., 2019; I. C. G. Vieira et al., 2014), it is eventually colonized by secondary vegetation. In the Amazon, around 21% of deforested land is covered by secondary forests (INPE, 2021). However, this secondary vegetation can be a closed-canopy forest, rich in mature species and biodiversity, or a degraded open-canopy forest, with a high incidence of drying agents (light and wind) and predominance of invasive grass and herbaceous species. The prevalence of one or another type of secondary forest will depend on the history of occupation of the area before and after abandonment.

In landscapes where the rain forest was widely converted into pastures prior to abandonment, colonization by invasive grasses dominates the first stages of the secondary vegetation establishment (Veldman, 2016; Veldman & Putz, 2011). The invasive grasses compete with young seedlings for light, reducing recruitment (Hoffmann et al., 2004). The use of fires as a management practice to clean pastures and fertilize crop fields reduces soil fertility and, consequently, the rates of recovery (Heinrich et al., 2021; Jakovac et al., 2015).

Human activities after the land abandonment also influence the structure and composition of the secondary forests. Secondary forests are almost two times more likely to be cleared than mature forests due to lower governmental restrictions and higher accessibility (Y. Wang et al., 2020). As a result, most secondary forests are cleared again before 20 years of regrowth (Chazdon et al., 2016; Jakovac et al., 2017; Schwartz et al., 2020). Furthermore, forest fragmentation associated with extensive land use systems causes tree dispersal limitations, reducing tree recruitment (Arroyo-Rodríguez, Saldaña-Vázquez, et al., 2017) and representing another amplifying feedback that might hinder secondary forest succession. Furthermore, repeated fires often kill most of the tree community (Balch et al., 2011; Brando et al., 2012; Cochrane & Schulze, 1999), particularly the younger trees, which also affects tree recruitment (Balch et al., 2011). Such practices cause secondary forests to persist in the landscape in an early successional state, dominated by fire-tolerant trees and palm species, together with invasive alien grasses and opportunistic herbaceous plants (Perz & Skole, 2003; Veldman & Putz, 2011). These areas can shelter only a small fraction of Amazon species diversity, thus resulting in impoverishment of the biodiversity (Lennox et al., 2018).

10.5.3. Transition to a Dominant Savanna Type: Savannization

The Amazonian savannization hypothesis describes another possible condition for the future of an Amazon forest strongly threatened by human activities and synergistic effects (Nobre et al., 1991). Unlike the replacement by secondary forest (also called "secondarization"), resulting from the spontaneous recovery of vegetation in deforested and later abandoned areas, as described above, the Amazon savannization process does not refer strictly to colonization by savanna species; rather, it refers to the differential survival of species with characteristics similar to those of savanna species (i.e., greater resistance to prolonged dry periods of >5 months and successive fires) over rain forest species (Nobre & Borma, 2009).

The Amazonian savannization hypothesis has mainly been tested using dynamic vegetation models, which simulate the dominance of a vegetation type under future climate scenarios (Lapola et al., 2009; Nobre et al., 1991; Oyama & Nobre, 2003; L. F. Salazar et al., 2007). Using a global atmospheric circulation model (CPTEC/COLA AGCM) coupled to a potential vegetation model (CPTEC-PVM), Oyama and Nobre (2003) found the existence of two stable equilibrium states in tropical South America for current climate conditions and a set of plausible future climate conditions. One of the states corresponds to the current distribution of the Amazon rain forest and savanna biomes. The second corresponds to a new equilibrium state, in which forest areas are replaced by savannas, especially in the eastern region. Scholze et al. (2006) quantified the risk of forest loss as a result of climate effects: A dynamic vegetation model (LPJ-DGVM) was forced with 52 scenarios and 16 climate models, mapping the natural variability of fire frequency and fresh water supply. The authors grouped the responses of ecosystems to warming by simulated amounts of less than 2°C, 2°C–3°C, and more than 3°C. The Amazon region is included among the areas that show increased risk of forest loss, with related increased savanna area and frequency of fire. Sampaio et al. (2007) found a tipping point when deforestation reaches 40% of the Amazon basin. When including synergistic effects of deforestation and climate change, this threshold decreases to 20%–25% (Lovejoy & Nobre, 2018). Hirota et al. (2011) and Staver et al. (2011) found that a tipping point could be reached if annual rainfall decreases to 1,000 mm. Finally, an increase of 2°C in the average temperature could also act as a tipping point for the Amazon Forest (Jones et al., 2009; Scholze et al., 2006).

Evidence of Amazon rain forest replacement by a savanna vegetation type has already been observed in two areas. The first includes the seasonally flooded areas of the Rio Negro (Flores et al., 2016, 2017). A shift into a native savanna state is likely to happen in those floodplains because they are more exposed to erosion (Flores et al., 2019). The second is at the transition zone between the rain forest and the Brazilian Cerrado (i.e., the deforestation arch). It is a sensitive region under many aspects. First, this region comprises the ecotone between Brazilian savanna and the Amazon region, where rain forests expanded over Cerrado and vice-versa along geological times and changes in climate; second, it is the region where the dry season is normally longer compared to the other Amazon regions and also the region where an increase in the severity of droughts (lower rainfall and prolonged dry period) has been observed; third, it is also a region under strong pressure of agricultural activities, which alter the forest structure and composition (Dexter et al., 2018).

10.6. The Role of Biodiversity on the Amazon Forest Resilience to Abrupt Change

The degree of resilience and hysteresis of a given ecosystem vary significantly with the type of driver. For the Amazon, forest response to change, resilience, and hysteresis can be quite different depending on whether the

anthropogenic change is fire, deforestation, extreme drought events, or climate change (Figure 6). Resilience and hysteresis responses will also be different when the system experiences synergistic effects of these drivers. For example, the occurrence of fire is greater and more harmful in the dry months and in areas that have been subjected to severe droughts (Aragão et al., 2007). Likewise, fire is accentuated at the edges between the forest and the deforested area, where uncontrolled fire enters more easily into the forest. The multiple drivers of anthropogenic changes in the Amazon region have been subjecting the forest to growing threats, raising concerns that these changes may be leading to a collapse of the ecosystem. A key question to address is whether interactions between stressors and disturbances will be large enough to exceed the capacity of tropical forests to resist and respond to such changes; or conversely, we can ask how great is the forest's resilience—its ability to maintain its integrity when subjected to disturbance (Holling, 2013). Some aspects of Amazon Forest functioning have been considered resilience factors. Here, we discuss, as potential resilience factors, the CO_2 fertilization effect, the deep-root water uptake mechanism, and biodiversity.

A mechanism previously considered to be a source of forest resilience in the long term is the so-called CO_2 fertilization effect. It has been theorized that the CO_2 fertilization effect could decrease the net loss of biomass caused by increased droughts. Basically, because plant stomata need to open less for assimilation of the same amount of CO_2 when atmospheric CO_2 is greater, the plant loses less water through transpiration, increasing water use efficiency and making it less sensitive to soil moisture loss (Lloyd & Farquhar, 2008). However, it is still unclear whether the decrease of transpiration on a large scale may have the potential to change the local precipitation. Another problem arising from CO_2 fertilization, according to Phillips et al. (2005), is the possibility that pioneer species such as lianas could gain an advantage with the increased CO_2 in the atmosphere. Since these fast-growing species have lower wood density, their competitive advantage could cause a decrease in the amount of carbon stored in the forest. Also, although additional CO_2 is expected to increase productivity, potentially accelerating tree growth at the cost of decreasing tree longevity across the basin (Brienen et al., 2015), low phosphorus availability may hamper these hypothetical productivity increases. Thus, the overall effect of CO_2 fertilization on forest resilience is still unknown (Fleischer et al., 2019).

An Amazon forest trait that has been considered to provide some forest resilience to drought is the assimilation of water from deeper layers of soil through deep root systems (Brum et al., 2019; Bruno et al., 2006; Hodnett et al., 1995; Jipp et al., 1998; Nepstad et al., 1994). However, while deep roots help to maintain the Amazon forest as evergreen, also maintaining photosynthesis (Myneni et al., 2007) and transpiration rates (Kunert et al., 2017), they do not figure as an important factor in resilience to severe droughts. In fact, several studies report that the larger trees, which potentially are older and have deeper roots, have high mortality rates during natural (Esquivel-Muelbert et al., 2020; Phillips et al., 2009) and induced droughts (Nepstad et al., 2007). That is because Amazon soils store soil water in very small pores (cryptopores) that make most of the soil water unavailable to plants when the soil becomes dry (Hodnett et al., 1995). Additionally, during the first years of a rainfall exclusion experiment in an eastern Amazon experimental site, the ability of the forests to take up water from deeper layers was identified as being responsible for the initial forest resilience shown. However, after around 3 years of wet-season suppression, the larger trees and lianas begin to die (Nepstad et al., 2007). These results challenge the idea that the deep-root water mechanism is an important factor in forest resilience to droughts.

Based on these findings, we consider the main and most indisputable factor in Amazon Forest resilience to be its huge biodiversity, through the respective biodiversity attributes of structure, composition, and function. The dense rain forest structure prevents excessive solar radiation and light entrance, maintaining moisture conditions and nutrient cycling rates. This dense structure also prevents the spread of fire, which is an important factor in selective forest loss and regrowth. Plant trait diversity may enable Amazon forests to adjust to new climate conditions, protecting their ecosystem functions (Sakschewski et al., 2016). Across the Amazon Forest, biotic diversity and abiotic heterogeneity promote a huge variety of plant responses to disturbances, promoting a balance between plant growth, survival, and mortality and acting as resilience factors. Also, diverse life-history strategies (e.g., fast-slow continuum in growth rates) have been shown to determine species-level mortality (Esquivel-Muelbert et al., 2020). Thus, we conclude that the diversity of functions derived from the biome's structural and compositional diversity is the most important factor underpinning the Amazon Forest's resilience to anthropogenic drivers that act synergistically, at local, regional, and global scales. Factors that threaten the attributes of biodiversity—namely, structure, composition, and functions—will strongly push the ecosystem into a second stable state, which is closer to an "impoverished savanna." Changes from the humid forest to a

subhumid forest can promote abrupt changes in the ESs delivered. One service of particular importance is the climate regulation service, which is promoted at large scale by the Amazon Forest but is not important in the Tropical Savanna (Table 5).

11. Implications for Global Tropical Forests

As discussed in Section 4, the distribution and biodiversity of the three major South American tropical forests have been shaped by large-scale geophysical characteristics, such as relief, climate, soils, and CO_2 concentrations. As a general principle, the structural dynamics of forest canopies and the ESs they provide involve complex interactions among these abiotic environmental characteristics, stand structure, species composition, and disturbance regimes. The same principle can be applied when contrasting South American forests with the other global humid and subhumid tropical forests and other ESs they provide.

Asian rain forests are mostly distributed across islands in Southeast Asia with average annual precipitation between 1,700 and 3,000 mm (Malhi & Wright, 2004). Despite this region's tropical wet climate, disruption of the monsoon cycle may result in widespread forest fires, such as occurred in 1997–1998 (Latif et al., 2017). African rain forests are the "the great green heart of Africa," and they present a unique combination of ecological, climatic, and human interactions (Malhi et al., 2013). The true rainfall regime of the region is uncertain, given the sparse and largely not operational ground meteorological observation system over the region (Washington et al., 2013). The same authors analyzed a range of model and satellite observation products for the region and concluded that they show little agreement in estimates of the region's distribution and the total amount of rainfall (e.g., whether the western or eastern Congo basin is wetter). The data sets differ by a factor of at least two, and in absolute terms by at least 2,000 mm per year.

Other differences in forest structure have also been identified. The understory of Asian tropical forest is mainly composed of large canopy saplings, while in Africa and South America, the prevalence of plants of lower stature at maturity is higher (LaFrankie et al., 2006). Below, we briefly discuss one comparative example of a tropical forest ES—the climate regulation service—across three global tropical forest regions.

Consider the climate regulation ES provided by the Amazon rain forest and its interaction with the relief. As explained in Section 5, the trade winds bring moist air from the Atlantic Ocean into the Amazon, which causes rains over the Amazon. The steady ET from the rain forest injects moisture into the atmosphere, continuously recycling the water vapor. Upon reaching the Andes, the mechanical uplift from the mountains and the Andes' concave shape facilitate high precipitation rates several hundred kilometers before the mountains and hinders moisture from crossing the Andes and leaving the basin.

In contrast, in central Africa, the annual cycle of rainfall is primarily dominated by the change of the atmospheric pressure system and is associated with the Hadley and Walker circulations (Longandjo & Rouault, 2020). The low-level westerly jet over the Atlantic Ocean, a lower branch of the Walker-like cell over central Africa, supplies moisture to central Africa inland (McCollum et al., 2000). Injection of water vapor into the atmosphere by ET and the role of orography do not seem to play important roles.

In Southeast Asia, the climate is typically monsoonal. The monsoon is a seasonal change in atmospheric circulation and precipitation connected with the heating of the land and ocean. The change in land and sea temperatures determines the condensation rate, resulting in precipitation. Warmer temperatures indicate more condensation of water vapor and higher rainfall rates, and vice versa (Levermann et al., 2009). In Southeast Asia, the humid forests are fragmented across several islands and relatively small pieces of the continent. In these circumstances, the continental recycling of water vapor is decreased compared to the massive continental area blocked off by high mountains such as the Andes adjacent to the Amazon.

Despite these differences, climate models have shown consistent reductions in precipitation when total humid forest cover was removed. Avissar and Werth (2005) have shown that, in full deforestation scenarios, precipitation in the Amazon, Central Africa, and Southeast Asia decreases during most of the year. Still, teleconnections to other land and ocean regions may increase or decrease precipitation for at least 3 months during the year, depending on the location. The most notable change in response to a full deforestation scenario is an increase in precipitation in the Arabian Peninsula due to African and Southeast Asian deforestation—most likely a consequence of changes in the Walker circulation.

12. Concluding Remarks

The tropical forests of South America generate ESs beyond the carbon-related services that benefit people globally. We reviewed the evidence of ESs provided by the Amazon Forest, Atlantic Forest, and Tropical Savanna biomes. Different types of tropical forests (i.e., humid and subhumid) produce many different types of ESs. While climate and freshwater regulating services are linked to the forest structure and composition, provisioning services, such as pollination and forest products, are closely linked to biodiversity. That is one reason why the ESs provided by the subhumid forests (savannas) differ from the ESs provided by the Amazon Forest. In terms of regulating and water provisioning services of the Amazon, forests stand out for their climate regulating ESs that benefit both South American and global populations. Elevated ET rates throughout the year are a constant source of vapor for the Amazon Forest and for the downwind regions in South America. The Atlantic Forest, despite being classified as rain forest like the Amazon, is more recognized for its services of water provisioning, erosion control, and slope stabilization than for its rainfall production. Nevertheless, it is important to consider that the Atlantic Forest encompasses very important mountain cloud forests that produce substantial rainfall. However, in this extensive review, we did not find studies related to the role of the tropical savanna (mainly Brazilian Cerrado) in rainfall production. That is probably because, despite their very high species richness (i.e., composition) the structure of the savannas strongly differs from the structure of the Amazon's forests. However, the Brazilian Cerrado is well recognized for its role in water production. Being located in the central plateau of Brazil, the Brazilian Cerrado acts as a kind of "water tank," storing rainwater in its deep and porous soils, then gradually releasing it in the dry period. The vegetation of the Brazilian Cerrado—including forests, shrubs, and grasses—is recognized for favoring the infiltration of rainwater that recharges water sources.

In terms of food provisioning, medicinals, and cultural services, we found no clear differences between the services provided by the humid and subhumid forests. That is probably because, unlike the regulating and water provisioning services, food provisioning, medicinals, and cultural services are more related to the species richness (i.e., composition) than to the structure of forests. In this sense, the greater the species richness, the greater the number of options for local people.

Our results also highlight the fact that, despite the importance of the rain forests for many ESs, these forests are facing major threats. Future prospects include the mortality of the Amazon's forests or the change to a different forest type that is more resilient to droughts and to a longer dry season. In other words, it means there is a risk that the Amazon rain forest will become more like savanna vegetation. The savannas, especially in the Brazilian Cerrado, are responsible for high biodiversity and several ESs. However, their structure and composition are less dense than the humid forests', and they are less effective than the latter in climate regulation by cooling and rainfall production. So, the loss of the Amazon Forest will portend profound changes in the services the region provides, especially climate services. Because of the large extent of the Amazon Forest—the world's largest block of nearly intact humid forest—these impacts could affect global climate functioning more strongly than the impact of a hypothetical release of their carbon stocks into the atmosphere.

To ensure the continuity of ESs provision from South America's tropical forests, it is essential that stakeholders are aware of the importance of these forests for providing such ESs and that they are empowered to act to preserve them. Local communities and small stakeholders have a large share of their well-being coming from forest ESs. Agribusiness stakeholders, however, are often willing to decrease their common benefit from ESs provision in exchange for a higher private economic benefit, often coming from agricultural expansion over forest land. Spatially explicit research approaches may contribute to identifying values held by the local stakeholders and the main actors involved for that region, thus providing information to aid governments in defining appropriate policies and tools for forest management.

Research on carbon-related services has led to a well-established approach to valuation and quantification of carbon sequestration, with global targets and information that allow the projection of climate change mitigation abatement costs and estimation of the carbon-related benefits of forest maintenance. Contrary to the example of carbon storage ESs, the noncarbon ESs are multiple, requiring several measurement strategies, and specific global targets are scarce. Their prices are not standardized, their value is more difficult to evaluate, and their provision/benefit ratio depends on where the provision comes from and where the beneficiary is located. Taking this into consideration, the complexity of outlining strategies that guarantee the provision of all noncarbon ESs maintenance costs is much greater than for carbon-related ESs. Environmental strategies to maintain the ESs

discussed here must be bold in terms of forest conservation goals—otherwise, these ESs could collapse before we are even able to define the tipping points at which the provision of these services will enter irreversible, declining pathways.

This article has demonstrated that the scientific literature provides overwhelming evidence of the importance of forest conservation for human well-being that extends beyond climate change mitigation. Nevertheless, it is important to further expand our understanding of the impacts of forest losses on different ESs using both ex post (i.e., changes that have already happened) and ex ante (i.e., losses that are likely to happen in different scenarios) approaches. It is also crucial to step up efforts to inform the creation of environmental policies as well as health, energy, and economic policies, given the close linkages of these fields with specific land uses. In this way, this body of literature should lead to the engagement of sectors of the economy that historically have seen forests as an obstacle to economic growth, rather than a green infrastructure providing ESs that are essential for the region's sustainable development.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Data were not created for this research. All data used are cited in appropriate places along the text and cited in the references.

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