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Neotropical Forests from their Emergence to the Future Scenario of Climatic Changes

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Abstract

Neotropical forests (NFs) play a main role in delivering environmental services such as biodiversity conservation and C sink. At the same time, these are some of the most disturbed vegetations in the world, since they are under accelerated rates of suppression and recovery. Conserving the remaining NF and recovering degraded areas is then urgent, although it is not an easy task. Ecological traits are widely varied across NF, as well as their responses to anthropic intervention. Generally, two large groups are observed according to climatic traits: (a) rain forests (RFs), in regions with 6 months or more of precipitation during the year and (b) seasonal dry forests (SDFs), in drier regions. Such forest types show very distinct species composition, α- and β-diversities, as well as functional and biomass dynamics. In this chapter, we both highlight the main differences between RF and DF, from their origin to present-day distribution, species composition, taxonomic and functional diversities, and discuss the predictions for shifts in all these traits during the next decades. Although few certainties, NF potential for mitigation of atmospheric C increases is a consensus among researchers. We also speculate about possible interventions, with the aim of avoiding a drastic future scenario.

Keywords: Anthropocene, C sequestration, deforestation, global warming, greenhouse effect, Gondwana, Latin America, selective logging

1. Introduction

Forests play a main role in global ecosystem services as water supply, climate regulation, conservation of biodiversity richness, and carbon dynamic and storage. In this way, they are at local, regional, and global levels, one of the most important mitigators of the environmental changes that characterize the Anthropocene era. In spite of this, changes on forest cover and

structure, most of them being deleterious alterations, are still being intensified throughout the world. For instance, 15.3 billion of the current 3.04 trillion living trees in the planet are vanishing annually [1], as a result, ~192,000 km^2 of forest area was lost per year, which means that 2.3 million km^2 of forest was depleted in the first dozen years of the present millennium. Unfortunately, numbers for global forest regrowth are more modest, with the regeneration of only 1.0 million km^2 in the same period. Deforestation impacts are still higher in the tropics, where forest loss is increasing in a rate of 2101 km^2 year^{-1} [2]. As this vegetation stocks a massive amount of 55% of the C of global forests (471 Pg), such dynamics results in a release of approximately 3 Pg C year^{-1} into the atmosphere [3], making their conservation an urgent issue. In this context, Neotropical forests (NFs) have a noteworthy function, as they hold almost 50% of the C pool in tropical forests [4] (**Figure 1**). Furthermore, these forests were although considered as a top priority for maintenance of global biodiversity [5], they are widely depleted for agriculture and livestock expansion in both Meso and South Americas.

Due to the huge area comprised by the Neotropics, one can imagine that forest conservation should not be an easy issue, requiring unmistakable strategies according to the distinctiveness on species composition and ecological traits of the vegetation. Indeed, heterogeneity of NF has been recognized for a long time, and many systems have been proposed for their classification. In a useful synthesis of such systems, five main forest physiognomies were proposed—broadleaved forest, mixed needle-broadleaved forest, stiff-leaved forest, broadleaved dwarf-forest, and stiff-leaved dwarf-forest—based on canopy structure and species
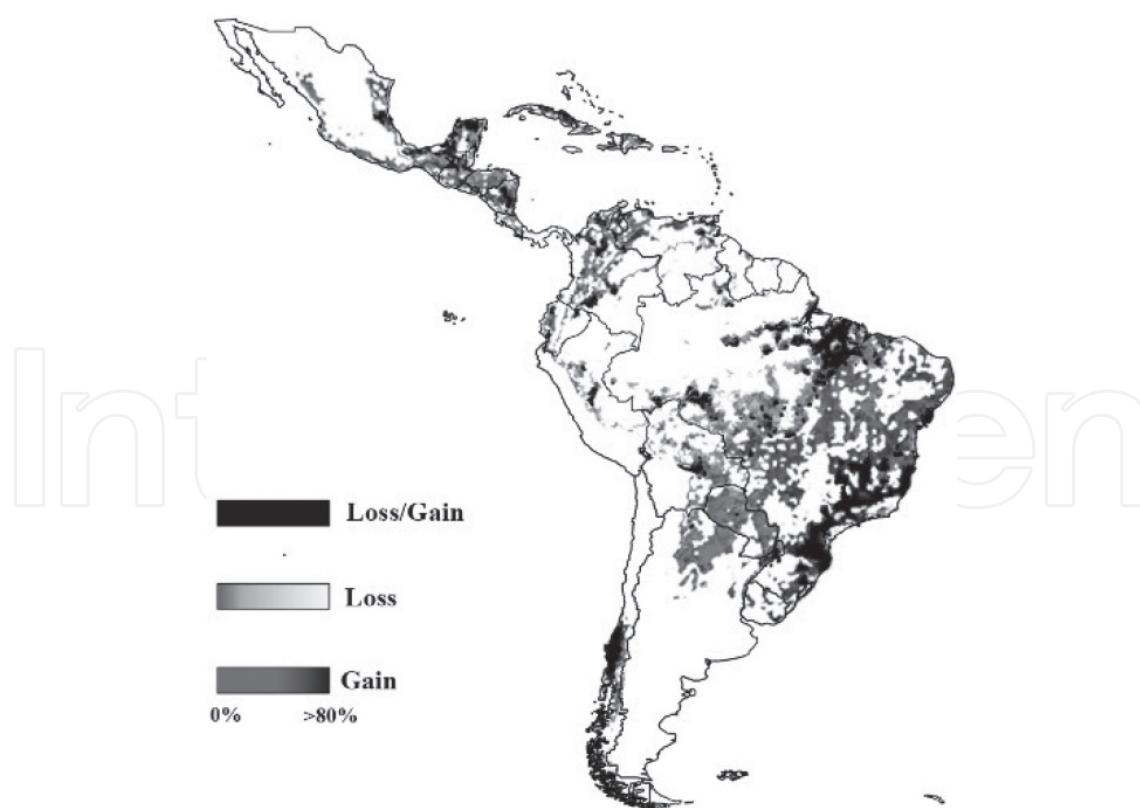

Figure 1. Extent of forest loss (red), gain (green), and both (magenta) for the 2000–2012 period, as stated by Hansen et al. (2013) [2].

assemblage [6]. The author, however, stresses that these criteria on their own are not enough to embrace all disparities of the vegetation and thus incorporates additional descriptors based on ecological and physiognomic attributes to be used in different combinations, as far as required. In consonance to this philosophy, many recent studies of biogeography, macroecology, evolution, and/or conservation recognize the average annual period for plant growth as the main attribute to delineate two main types of Tropical NFs, which we also adopt here: (a) seasonal dry forests (SDFs, are those occurring in regions with <1800 mm of annual rainfall and at least 5–6 months with less than 100 mm) [7] and (b) rain forests (RFs, are those occurring under more than 1800 m of mean annual precipitation, mean annual temperature >18°C, and seasonal variation in temperature lower than 7°C) [8]. It is important to highlight that water availability is determined not only by rainfall regime but also by variations of ground water regimes related to soils and geomorphology. Therefore, forests under different precipitation conditions may have similar growth periods, species compositions, and ecological traits [9]. It must be also stressed that the RF and SDF concepts are expanded here to include the southern temperate NF in spite of their strikingly distinct flora and environment [10].

In general, the larger continuous extents of NF are found as RF, although both patches and incursions are not uncommon. On the other hand, SDFs show a predominantly patchy distribution, with a wide variation in patch size [11]. Contrasting with SDFs, RFs display a lower species turnover, despite the intense plant migration favored by the instable conditions of those very dynamic communities. Notwithstanding the impressive α-diversity, the β-diversity of RF is low compared to that of SDF. Besides this, the γ-diversity in RF is high, due to the variation on species pools among geographically isolated patches. Opposed to this, the more stable SDF have a low rate of migration events, leading to higher levels of endemism. Despite the much lower α-diversity of SDF, the genetic variation of populations is commonly higher.

It is unfortunate that a low percentage of the Neotropical forests is under legal protection, with less than a quarter of the RF and just 4% of SDF, and, awkwardly, both of them are at present-day agriculture and livestock frontiers [12–14]. While the high turnover of species in continental, regional, and local scales is an inherent challenge for biodiversity conservation of the SDF, the growing fragmentation is a current threat to the maintenance of diversity and recovery of degraded areas in both NF and RF [15]. Additionally, current environmental changes—such as global warming associated to increased drought severity—may boost disturbance events and tree mortality and lead to the development of novel ecosystems, where hitherto NFs were dominant. Predicting how species and communities will behave in this scenario is thus a priority for successful actions of conservation of both Neotropical RF and SDF in the next decades.

2. Evolution of the Neotropical forests

It is widely accepted that most of the NF flora has evolved from a Jurassic Gondwanan pool, where cool-temperate vegetation, constituted principally by a conifer-tree/fern forest community, was found [16]. By late Cretaceous, however, the radiation of flowering plants changed this flora to that of more or less broadleaved and evergreen forests, with a differentiation

between the northern and southern Gondwana land masses. The Sub-Antarctic fraction of the super-continent was quickly and almost completely dominated by angiosperms, while the Austral held down elements of the temperate vegetation, giving rise to the so-called Gondwana Paleovegetation. While the first represents the pristine source of diversity for the present South American tropical forests, the latter is considered the ancestral of the present forests of the humid and cool-temperate south. Indeed, many ancient lineages of the mixed paleo-flora, as Araucariaceae, Cunoniaceae, Lauraceae, Myrtaceae, Monimiaceae, Nothofagaceae, and Podocarpaceae, can still be found in southern South America despite the drastic changes that took place during the Paleocene [8]. During the Cenozoic Paleocene-Eocene Thermal Maximum, the Austral-derived flora started a migration toward lower latitudes, reaching the southern borders of the tropics. This process continued during the subsequent warming events until the Early Eocene Climatic Optimum, when both temperate and tropical forests expanded and experienced intense *in situ* speciation events. Tropical plant diversity then rose incredibly, with speciation surpassing extinction at around 30%. Despite the high speciation rates in the tropics, such processes also took place independently along the latitudinal gradient beyond its limits, leading to a specially diversified set of clades. The already recognizable Neotropical rainforests were also expanding, with a few lineages reaching the extratropical South America, and, at the same time, elements of the Northern Hemisphere were also reaching the tropics after the uplift of the Mesoamerican isthmus [8, 17].

The warming events of the Eocene intensified the expansion of the tropical flora, but it is very likely that forest communities as a whole could not invade or coexist with the temperate forests, as the southern flora at that time lacked most of the clades that were abundant in the tropics (e.g., Anacardiaceae, Annonaceae, Euphorbiaceae, Meliaceae, Moraceae, Sapotaceae, Violaceae, and Zingiberales) but were rich in families rare anywhere else (e.g., Akaniaceae, Atherospermataceae, Casuarinaceae, Cunoniaceae, Myrtaceae, and Proteaceae) [8]. With the rise of the Andean Chain in the Neogene, new marked changes took place in the South America flora. In the South, many lineages became restrict to the pacific side of the mountains, as well as extinction processes occurred (e.g., *Casuarina* and *Eucalyptus*), and another expansion northwards was initiated, this time crossing the tropics frontier and occupying the recent emerged mountainous areas [18]. Regarding Amazon, the area became much more dynamic leading to the emergence of much more heterogeneous traits, which drove the diversification of many clades [16, 19]. Further climate changes along Neogene and Pleistocene drove the consolidation of the RF and SDF nuclei, despite their areas waxed and waned following the fluctuations of both rainfall and temperature. It is believed that before the glacial maximum of the late Pleistocene, the tropical Neotropics was mostly covered by forest formations, and that SDF widely dominated the Dry Diagonal during the Pleistocene Glacial Maximum. They were probably not continuous at that or any other time, which is reflected on the current scarcity of widespread species throughout SDF islands [7]. Yet, the presence of many populations at the same SDF nuclei for many million years indicates that core areas have been preserved over time. Nonetheless, it is very likely that SDF had expanded into RF domains along both the Pleistocene and the late Holocene Last Glacial Maximum, favored by the cooler and dryness of such periods. After the Last Glacial Maximum, tropical SDF suffered many events of expansion and contraction, being the broader expansion reached on the mid-Holocene dry interval (~5000 years ago) [9].

Rain forest areas, unlike those of SDF, used to diminish during the Quaternary glaciations, when they became, at higher or lower levels, fragmentated and confined into refugia islands [20, 21]. The matrix surrounding these patches suffered varied alterations, with part remaining forest (SDF) and part being covered by other vegetation types, particularly grasslands and savannas. Migrations across South America indeed occurred during such periods, including the establishment of the Andean *Alnus* and *Podocarpus* into the central Amazonian lowlands. Because of the reduced temperatures, precipitation, and atmospheric CO_2 of the Last Glacial Maxima, the Amazonian forests were less productive, had lower canopy structure, and were floristically and distinct than those of today. The basin area was predominantly covered by forests and was affected in different ways by the climatic changes. Vegetation at the western catchment area remained part of the Intertropical Convergence Zone and was less impacted, while the southern/eastern RFs were liable to drier and longer dry seasons and were mostly replaced by SDF or savannas [22]. Fire had an important role on species control during the subsequent expansion and contraction cycles especially at the southern/eastern regions RF [23]. Such processes probably influenced the present gradient of RF biodiversity within the basin. On the Late Holocene, RF reached their widest distribution, as a response to the increased precipitation caused by greater austral summer insolation. Fire outbreaks increased in the drier periods of the Holocene, resulting in the exclusion of a set of species from the most affected areas and thus taking part in the modulation of the present-day biogeography of Amazonian. In the following dry periods of the early-mid Holocene, such forests contracted again until reaching the current configuration—or that of the European arrival [19, 24]. Rain forests of the Atlantic domain were also impacted by the Pleistocene and Holocene climatic fluctuations, provoking the emergence of many C4 lineages during the drier periods, especially at the Last Glacial Maxima. After that, Atlantic RF experienced a big expansion and had the representativeness of gymnosperms diminished, being likely, then, that Atlantic Forests reached its modern floristic composition on the early Holocene [25, 26].

The Late Quaternary Extinctions of the South American megafauna (~50,000–10,000 years ago) might also have contributed to changes on the NF vegetation and flora [27]. For example, the dispersal processes of the zoochorous species were probably affected, particularly for those bearing large fleshy fruits, perhaps leading to the extinction of part of them. Because most of these should have been of climax species, their decline could have affected the dynamics of forests as a whole. In addition, litter amounts probably increased with diminished herbivory, and, consequently, enlarged fuel loads and fire frequency/intensity—a process significantly raised during the last 9000 years by the human arrival in the Neotropics [28]. Quaternary fires might have partially and temporarily suppressed or disturbed specific regions of RF, which are nowadays less diverse. Contrary to what one may think, this process probably has not favored SDF establishment, which is indicated by the absence of fire adaptations in their present-day flora [7]. Nonetheless, the anthropogenic impacts that took place afterward certainly surpassed by far those promoted by fire, with significant suppression of both SDF and RF registered since the development of the first American cultures. Besides this, such processes were greatly intensified after Spanish and Portuguese occupation, when RF exploration was also initiated [13, 14]. Changes in such vegetations are still occurring in an accelerated rate, and increasing our knowledge on the response of NF to these threats is urgent whether we are legitimately interested on their conservation.

3. Neotropical forests: a complex vegetation mosaic

Notwithstanding the fact that the plant cover has gone through striking variation along the geological eras, forests were always well represented in the Neotropics. In fact, Europeans found massive extents of forests in both Meso and South Americas, when they arrived in those continents (**Figure 2**). The distribution pattern of both RF and SDF of that period can still be noted, although much of the plant mass has been depleted or modified in structure and connectivity. In general terms, RFs are found in areas with humid climates, independently of pedologic traits or flooding regimes [9]. Areas with prominent dry periods, depending on the existence of enough water supply and/or suitable pedologic conditions, may harbor either RF or SDF, respectively. Contrastingly, drier areas with low ground water and fertility are usually covered by either savannas or grasslands. Therefore, RFs are still found on the vast Amazon domain and on the Atlantic, Pacific, and Caribbean windward coastlands—the latter three much more fragmented than original [14]. Additionally, RFs are also found as riverine seasonal forests across drylands, as well as temperate rain forests in the Southern Cone [10, 29]. The scattered distribution SDF concentrates across the so-called Pleistocene Arc that surrounds the Amazon basin before stretching into Mesoamerica and the Caribbean [11, 15, 30].

Rain Forests   **Seasonal Dry Forests**

Figure 2. Extent and geographical distribution of Neotropical forest domains (solid patches; discontinuity within domains are not considered) and incursions in other domains (spotted areas). Adapted from Jaramillo and Cárdenas (2003), Fernandez-Vega et al.(2017) [14], and Rezende et al. (2017) [10].

Originally, RF covered more than half of Mesoamerican lands, where they had a somewhat discontinued distribution. Although human occupation increased their fragmentation, RF still occupies 30% of the isthmus area [14]. Regarding South America, almost half of the continent used to be covered by RF, with the Amazonian forest corresponding to a third of the continental area [8].

The Amazonian domain has a high α-diversity, though with a small set of trees (227 species) dominating all across [19]. Species composition and richness, however, vary widely in the region, with a notable increase in species richness toward the Andes [31]. Considering the botanical families, around 50% of the tree species belong to a small group formed by Leguminosae, Moraceae, Annonaceae, Euphorbiaceae, Lauraceae, Sapotaceae, Myristicaceae, and Arecaceae. Four out of these eight families are also well represented in terms of stem density, with around 60% of the trees belonging to Leguminosae, Arecaceae, Rubiaceae, Violaceae, Euphorbiaceae, Meliaceae, Sapotaceae, and Moraceae [8]. Some of these families are distributed in abundance gradients along the whole Amazonian region. For example, both Leguminosae and Burseraceae increase from the southwest to the northeast, where the well-represented Leguminosae may account for almost a quarter of the trees. In small scales, some families can show distinct distribution patterns, as that found for Lecythidaceae in French Guyana [32]. The second largest extent of RF is found along the South American Atlantic coast, namely the Atlantic domain, which extends from north-eastern Argentina and eastern Paraguay to north-eastern Brazil (**Figure 2**). In this domain, environmental traits are strongly influenced by the long latitudinal range, the mountainous terrain, as well as the sharp climatic gradient toward the continent hinterlands, conferring to the region more environmental contrasts than those across the whole Amazonian domain [33]. Those forests are home to a great β-diversity, resulting from high levels of both endemism and α-diversity, although a small number of species may be locally dominant [34]. Therefore, the Atlantic domain harbors not only RF but also other vegetation types, particularly where it finds its environmental limits. The following main types of RF may be distinguished accordingly: rain, cloud, rocky cloud, and Araucaria (mixed) forests, which are considered the core area of Atlantic forests. Semideciduous forests and rocky dwarf-forests are the predominant vegetations of the inner limits of the Atlantic domain, whose marginal habitats harbor almost half of the species endemic to the domain [29]. Many species from the Atlantic SDF and, less frequently, from the RF are found on the tropical and subtropical riverine forests that extend into the neighboring drier domains. Additionally, several species from the Amazonian RF are found in those riverine forests, which can be considered a floristic link among all disjunct South American RF [9, 35].

SDF are widely but discontinued distributed across Neotropics, and differently of RF, they lack both a latitudinal diversity richness gradient and many widespread species but always present a high β-diversity at both species and family levels. While they occupy almost a quarter of South America, they have a reduced representativeness in Mesoamerica, south of Mexico [7, 8]. Regarding the most representative families, Leguminosae hosts by far the largest number of species, followed by Burseraceae (particularly in Mexico), Cactaceae, Capparaceae, Erythroxylaceae, Malvaceae (Bombacoideae), and Zygophyllaceae (especially in Central America). Several clades have their species concentrated in or confined to Neotropical SDF. Many species are endemic to a specific region and belong to ancient lineages, most of which are monophyletic. Even when polyphyly is noted, the sister species are often found in

the same region, indicating a high geographic phylogenetic structuration. Besides that, the endemics tend to be abundant, resulting in a metacommunity pattern of high mid abundance levels [7]. There is a notable discontinuity among SDF islands, apart from both extremes of the Dry Diagonal, namely the Caatinga and Chaco domains, in north-eastern and central-southern South America, respectively (**Figure 2**) [36]. Within SDF domains, soil traits can be very important to determinate the deciduousness degree, with evergreeness as an efficient strategy to save input nutrients under oligotrophic conditions [37].

It is believed that the Neotropical SDF of the South American Dry Diagonal had a much more continuous cover during the Pleistocene Glaciations [30]. Significant floristic differences are currently found among the three domains in the region, namely the Caatinga, Chaco, and Cerrado, which is the Brazilian savannas domain, where many incursions of SDF are found [36]. In some cases, the number of endemics can be high, as in Caatinga, within which a rocky portion can be discriminated due to the abundance of some species, belonging to four families: Cactaceae (*Brasilicereus phaeacanthus*, *C. albicaulis*, *Facheiroa squamosa*, *Pereskia aureiflora*, *P. bahiensis*, *P. stenantha*, *P. glaucochrous*, *P. pentaedrophorus*, *Stephanocereus leucostele*), Euphorbiaceae (*Cnidoscolus bahianus*, *C. argyrophylloides*, and *Jatropha palmatifolia*), Leguminosae (*Blanchetiodendron blanchetii*, *Mimosa irrigua*, *Poincianella laxiflora*, *Pseudopiptadenia brenanii*, *Pterocarpus villosus*, *P. zehntneri*, and *Pterodon abruptus*), and Rutaceae (*Galipea ciliata* and *Pilocarpus sulcatus*). In the case of the Cerrado, the number of generalists is increased because of the numerous tree species shared with the co-occurring savannas and riverine forests, which contribute to the higher species richness in the domain. A number of species are common throughout the Dry Diagonal, such as *Anadenanthera colubrina*, *Myracroduon urundeuva*, *Handroanthus impetiginosus*, *Aspidosperma pyrifolium*, *Senegalia polyphylla*, *Amburana cearensis*, *Schinus brasiliensis*, *Annona leptopetala*, and *Platymiscium floribundum*.

The remaining South American SDFs, occurring from northern Argentina to the Caribbean coast of Colombia and Venezuela, show similar patterns, despite the occurrence of a few distinct species groups. Venezuelan SDFs, for example, include *Bourreria cumanensis*, *Erythroxylon havanense*, *Guapira pacurero*, and several distinct species of Bignoniaceae, Boraginaceae, Capparidaceae, Euphorbiaceae, Leguminosae, Flacourtiaceae, Malpighiaceae, Rubiaceae, Rutaceae, and Sapindaceae [37]. However, there is also a great floristic variation as only a third of the botanical families are found throughout. This includes, for instance, increasing abundances toward the east of *Acacia tamarindifolia*, *Amaioua guianensis*, *Bourreria cumanensis*, *Bunchosia mollis*, *Bursera simaruba*, *Capparis verrucosa*, *C. tenuisiliqua*, *Cordia dentata*, *Croton choristopelis*, *Malpighia glabra*, *Piscidia carthaginensis*, *Pithecellobium oblongum*, and *Tabebuia chrysanta*, while *Acacia glomerosa*, *Amyris ignea*, *Chlorophora tinctoria*, *Fagara monophylla*, *Guaiacum officinale*, *Lonchocarpus violaceus*, *Morisonia americana*, *Trichilia hirta*, and *Vitex compressa* are very common in the north. The north also includes *Bourreria succulenta*, *Helietta pleeana*, *Krugiodendrum ferreum*, *Linociera caribaea*, *Pseudobombax septenatum*, *Zizyphus cinnamomum*, and the association of *Bursera* and *Lonchocarpus*, which are also very common in the Caribbean but rare across Venezuela.

RF and SDF floras of the temperate South America are strongly distinct of their correspondents in the tropics [8]. While Atherospermataceae, Winteraceae, Cunoniaceae, and Proteaceae are

some of the most abundant families, they are scarce in the tropics. At the same time, many of the major tropical clades as Anacardiaceae, Annonaceae, Meliaceae, Moraceae, and Sapotaceae are absent in temperate lands. Monotypic genera are more well-represented in the southern flora, with several of them even belonging to monogeneric families such as Aextoxicaceae, Desfontainiaceae, Eucryphiaceae, and Gomortegaceae. In this way, many lineages, such as *Aextoxicon*, *Citronella*, *Cryptocarya*, *Drimys*, *Gomortega*, *Laurelia*, *Persea*, *Laureliopsis*, *Legrandia*, *Nothofagus*, *Pitavia*, and *Podocarpus*, have diversified outside the tropics, keeping their ancestral preference for temperate conditions. Although the southern floras are considerably poorer than their tropical counterparts, they have a higher lineage diversity, that is, they hold more diversity on broader groups, such as families, which means older diversification with higher conservatism of clades in the temperate floras [10, 18]. There is also a high conservation of ancestral genetic polymorphism in SDF, which is due to factors such as their arrested dynamics (see session V), low immigration rates, and notorious discontinued distribution, whose combination results in a long persistence of SDF populations and also increasing the endemism levels [11, 38]. Tropical RFs, otherwise, have been experimenting intense diversification in more recent times.

4. Neotropical forests floristics and diversity are controlled by environmental and anthropic traits

There is a high floristic uniqueness in both the tropical and temperate NF, with species richness by far higher in the former due to higher speciation and lower extinction rates overtime. On the other hand, the temperate flora has a higher lineage diversity, that is, richness of ancient clades [10]. Despite these contrasts between both tropical/temperate and RF/SDF floras, some patterns are common to all, especially with regard to family distributions. For example, warmer temperatures and higher rainfall increase species richness for both Leguminosae and Bignoniaceae, cooler temperatures for Asteraceae and Melastomataceae, and dryness for Polygonaceae, while abundance is favored by lower temperatures for Melastomataceae and Rubiaceae and higher precipitation for Arecaceae [39]. However, to our knowledge, there are no studies on the main modulators of the present-day clade distribution for the temperate Neotropics.

The main driver of forest type distribution across the Neotropics is the rainfall regime, although the temperature plays a major role in the subtropical and temperate sectors [18]. Indeed, rainfall itself controls forest structure, species richness, and successional dynamics. Together with soil fertility and landscape heterogeneity, temperature has also a positive correlation to taxonomic structural complexity, expressed as an increasing gradient of species, genera, and families richness from SDF to RF [35, 38, 40]. Species richness among SDF islands is poorly affected by changes in the amount of precipitation; otherwise, water restriction seems to be very important for the maintenance of SDF patches, preventing the establishment of RF [7, 35]. Surprisingly, despite the leading role of rainfall for most patterns in the tropical sector, variations in temperature are the main control for family diversity, in both abundance and species richness.

Several climatic features also modulate species distribution at and within regional levels. For example, temperature seasonality is the main controller of tree species composition in the subtropical sector of the Atlantic domain, particularly segregating Araucaria-dominated forests [18]. In the tropical sector, water deficit severity and mean annual precipitation are the best predictors of changes in species composition, segregating two main floristic groups, containing (a) rain, cloud, and cloud dwarf-forests and (b) riverine and semideciduous forests and campos rupestres [29]. Additional roles are played by fire and frost frequency in segregating the woody flora of rock outcrops, as does strong winds and salt-spray for coastal white-sand woodlands. Likewise, rainfall patterns are the main controllers of species richness across the Amazon domain, with higher figures in the much rainier west and center than in the seasonal and drier east and south [19, 31].

The existence of forests across the Dry Diagonal depends basically on two factors: higher soil moisture on valley bottoms harboring riverine seasonal forests and patches higher fertility soils covered on either deciduous or semideciduous forests [9]. On top of this, climate features play an additional role, affecting the species composition of SDF across the whole Diagonal, and extremes of cold temperatures and dry season severity are key factors. Annonaceae, Bignoniaceae, Leguminosae, and Moraceae, less able to cope with freezing temperatures, are more abundant and diverse in the warmer northern sector, while Capparaceae, Leguminosae, and Polygonaceae are favored in drier areas and Annonaceae, Arecaceae, Moraceae, and Rubiaceae in moister ones [30]. In addition, in the warmer northern sector, soil mineral nutrients are almost as important as ground water availability in determining changes in species composition [36].

Nonclimatic environmental traits, such as space, altitude, substrate, topography, soil composition, as well as anthropic impacts, are very important in determining NF types across other geographic regions. In this way, in north-western Argentina, the chief explanatory variables for species distribution on the Andean piedmont slopes are related to increasing moisture and decreasing temperature toward higher altitudes [41]. For example, the moister the area, the higher the abundance of *Diatenopteryx sorbifolia*, *Ocotea puberula*, *Cordia americana*, and *Eugenia uniflora*, while the opposite pattern is shown by *Calycophyllum multiflorum*, *Phyllostylon rhamnoides*, *Astronium urundeuva*, and *Anadenanthera colubrina*. In Venezuelan SDF, rainfall decrease is positively related to increasing abundance of Mimosoideae, Cactaceae, and Capparaceae (*Capparis hastata*, *C. linearis*, *C. odoratissima*, *C. flexuosa*, and *C. pachaca*), which harbor several physiological adaptations, such as relatively deep root systems and low hydric potentials [37].

At more local scales, where many environmental traits, such as rainfall regimes and soils, can be much homogeneous, the best predictors of beta-diversity are commonly land-form-related variables, as in the case of French Guyanese RF, where the distribution of plant taxa is mainly modulated by geomorphological features [32]. Lecythidaceae and Caesalpinioideae are predominant in the coastal plains and hilly hinterlands, while Burseraceae, Vochysiaceae, Simaroubaceae, and Mimosoideae are predominant in valley bottoms. Mimosoideae are more diverse and abundant in mountains, even surpassing Lauraceae, typically diverse in Amazonian mountains in general.

It is known that forest dynamics related to single and multiple-tree falls largely contribute to variations in tree species composition in RF. The emergence of gaps creates opportunities for

the establishment of species belonging to different successional groups. Fast-growing and soft-wood tree species prevail immediately after gap creation and are followed by the emergence of the hard-wood species, which slowly become dominant in the canopy. However, these frequent and autogenic disturbances are not the only controlling factors of forest dynamics [14]. Indeed, other modes of disturbance may be important modulators of species composition, forest structure, and dynamics in certain sectors of the Neotropics. This includes severe ones, like hurricanes, convectional windstorms, severe droughts, fire outbreaks, floods, volcanic eruptions, landslides (caused by either rainstorms or seismic activities), and others of relatively moderate impact, such as droughts, fires, and shifting cultivation and regular winds. These impacts often interact, as in the case of wind frequency and strength, which increase in disturbed forests favored by discontinued canopy.

5. Modeling floristic and biomass dynamics in rain and dry forests

Forest communities along succession can be characterized according to the acquisitive or conservative traits of their populations, with regard to the economy of environmental resources. Conservative species can save limiting resources, such as water in drylands, while the acquisitive are not able to survive in restricted conditions of a given resource. In early successional stages, light is not a constraint factor in both RF and STDF, unlike water availability, which is a restrictive trait in SDF [38, 42]. Thus, conservative species are favored in the colonization of drylands, while there is no restriction to both functional types in humid areas. Anyway, acquisitive species are more competitive in RF because of their light-wood and related faster growth than that of the conservative hard-wood species. As succession goes on, RF environments get more light restrictive, favoring the growth of conservative shadow-tolerant species. On the other hand, for the less stratified SDF, warmness and dryness are both lessened after the pioneer community established, without significative restriction of light availability, which favors the arrival of the acquisitive species. As the conservative community grows up in RF, the light-demanding pioneer community starts declining, rather unlike the SDF where both functional groups are favored [38]. RF communities are very dynamic and, from the beginning of the death of conservative individuals, which starts earlier than in STDF, the proportion of functional groups is sustained overtime, despite their turnover on frequently opened areas. SDFs are more stable because of the increased longevity of their conservative individuals, and their gaps are smaller because of the smaller number of trees ripped off in the process. In addition, the re-sprout of neighboring living individuals is usual, while seedling survival rates are inexpressive. This scenario brings two main consequences for tree dispersal and species composition: (a) despite of the long-dispersal capacity of many SDF species, both dispersal of endemic species and the arrival of immigrants are hampered within their areas and (b) RFs are liable to both occurrences, and most of their species are not able to colonize SDF systems.

Such changes in functional composition and community structure are highly correlated to the above-ground biomass (AGB) dynamics, and as they are feedback-regulated by environmental traits, AGB dynamics is also distinct in RF and SDF. On early RF succession, when neither

light nor humidity are limiting factors, the fast-growing light-wood species correspond to the majority of the AGB. Thus, the shadier the environment becomes, the more competitive become the hard-wood and slow-growing species, resulting on both loss of light-wood trees and accelerated rates of biomass accumulation. Before the proportion of functional groups is stabilized, increasing accumulation rates of AGB are still observed overtime, due to the growth of hard-wood trees. On the other hand, after the establishment of the pioneer and long-lasting hard-wood SDF community, successional events give rise to either the arrival of small amounts of light-wood trees or the sprouting of the slow-growing ones [11, 38]. Thus, there are two factors involved on differentiation of biomass dynamics: (a) both earlier and later succession groups in each forest type belong to different functional groups; and (b) while the pioneer community is quickly replaced in RF, mortality rates of hard-wood early community in SDF are low until most advanced regeneration phases. The combination of these two factors create divergent patterns for both individual biomass contribution and the increase on AGB rates overtime: (a) RFs present continuously rising gains in AGB accumulation during a long time, until very late-successional phases, when the mortality of some hard-wood individuals reduces those gains and (b) the rhythm of biomass accumulation in SDF is slowly accelerated since the early successional phases, and this acceleration becomes irregular in the more advanced phases, when increases in AGB accumulation rates due to both colonization and sprout may not surpass the decrease due to loss of old hard-wood trees.

Since the abundance of functional groups is strongly dependent on tree recruitment, growth, and mortality, these are also important drivers for biomass dynamics. AGB gains due to tree growth is the key factor on the modulation of biomass increase in intact RF and SDF, corresponding to almost 50% of the variation within all successional groups [38]. The biomass loss due to mortality has a secondary role, and, as described above, it is important since early successional phases of RF, as well as in late regeneration phases of SDF. Notwithstanding, since these processes are under environmental control, their importance in community dynamics is currently being altered by the recent climatic shifts. Brienen et al. [43] claimed that the elevation of atmospheric C concentration overtime is inducing a continued gain in productivity in Amazonian forests and accelerating the individual life cycles, leading to a great rise in the number of dying trees. Indeed, the authors reported that this process is the major contributor to the decrease in the C sink capacity of such vegetation since the 1990s. Nonetheless, despite of the fact that the average basal area of that vegetation decreased overtime, the importance of big trees death for reducing AGB accumulation rates is not so high. On the other hand, they also outlined that the exceptional dryness of both 2005 and 2010 should be responsible for the increase of the mortality of large-stature trees in Amazonia in those years. In the same way, [44] demonstrated that annual seasonality is directly linked to fluctuations of recruitment rates in Mexican SDF, which were higher during the moist season, when gains on biodiversity were also noted. However, increases in recruitment, growth, and species richness were not observed in those SDF during the rainy 2006 and 2007 years that followed the dry 2005. It is likely, then, that severe droughts lead to the depletion of water and carbohydrates and that some time is required for full recovery. It is probable too that such climatic events may lead to shifts in ecological relations as herbivory, pollination, and dispersal that also modulate recruitment, growth, and species composition of plant communities.

6. Environmental and anthropic drivers of biomass dynamics in Neotropical forests

Taxonomic diversity is a strong modulator of AGB pools along tropical forests. Together with the functional dominance, which is the ponderation between the average of a functional trait and the relative abundance of a given clade in the community, taxonomic diversity explains almost 40% of the differences in the tropical forests C pools [45]. Along the Neotropics, however, besides the great variety in biomass and biodiversity, the correlation between them is weak. In this way, the species composition along NF, as inferred from its correlation with wood density functional dominance, is not correlated to AGB stocks within the vegetation. Anyway, this correlation can be observed at small scales because of niche complementarity in areas smaller than 1 ha [31]. Nevertheless, community structure, represented by the maximum diameter functional dominance, is a key driver for the differentiation of RF and SDF according to their C storage potentials [38]. Likewise, there is a high variation of forest structure in regional scales within these forest types, and, in combination with other traits, it can also control their AGB. An interesting example is found for Amazonian intact forests: (a) the more dynamic tree communities are, the lower is their average wood density; (b) the less dynamic peripheral areas also show lower average basal areas; (c) the integration of these features produces a gradient of decreasing AGB toward those peripheries [46]. Curiously, taxonomic diversity richness distribution follows this same biomass gradient [19], but further investigation is needed to confirm this as a pattern for the Neotropical RF.

NF cover is currently undergoing unprecedented changes. For instance, while forest regeneration is observed in many sites of highly impacted RF (**Figure 1**), appalling deforestation rates grants SDF the title of "most supressed woody ecosystem in the world" [2]. Anyway, together with the increasing number of degraded areas, the sites in regeneration are also increasing, boosted by their high regrowth potential [47]. As an example, C sequestration rates by secondary NF in 8 years were more than 10 times higher than that of the preserved Amazonian RF, reaching impressive rates of 3.05 Mg C ha^{-1} year^{-1} in average. Likewise, in a period of two decades, secondary forests were responsible for the rise of 122 Mg C ha^{-1} on the total AGB in the Neotropics, then becoming the major global contributor as a C global sink, despite the usually higher AGB pools of mature forests [48, 49]. In this way, a scenario of increased reforestation would easily improve the Neotropical C sink capacity. However, the actual situation is not so auspicious. For example, during the century, while C sequestration by secondary forests rose on a rate of 0.05 Pg C year^{-1}, the contribution of well-established forests to the C sink was reduced in 0.23 Pg C year^{-1}, and C emissions by deforestation increased on a rate of 0.14 Pg C year^{-1} [3].

Land use history has a key role on NF recovery rates. In this way, areas with denser tree residual tend to show quicker forest resurgences than those with no arboreal cover [12]. At the same time, the potential to increase the biomass pools also depends on the percent of forest cover of the surrounding matrix, the proximity to other fragments, and the time of regeneration [50]. In addition to this, environmental traits as rainfall regime, and other climatic features related to it, are key modulators of biomass, because they directly influence the growing season,

while soil traits play a supporting role, modulating the possibilities of returning to the climax structure [48, 51]. Much varied rates of AGB recovery are found among NF, both between RF and SDF, and within them. For example, rates from 4.7 to 6.1 Mg ha^{-1} year^{-1} in RF and from 2.3 to 1.9 Mg year^{-1} in SDF were observed, with the average AGB variation corresponding to shorter and longer periods, respectively [38]. Interestingly, functional traits found for SDF communities were claimed as positively correlated to regeneration of NF as a whole [48]. For the authors, the abundance of old tress belonging to hard-wood pioneer species in disturbed sites would be positive modulators of the time and rates of biomass recovering, while data of a Mexican SDF, where no clear correlation was found between regrowth span and regeneration rates, also suggest that it is not likely that time is an important controller of this vegetation [44]. Otherwise, the community structure at the beginning of the recovering process, as expressed by initial AGB or basal area, was found as strong modulators of biomass increases in RF, also influencing both the litter productivity and decomposition [31, 52].

7. Neotropical forests facing the Anthropocene era

Great human impacts on NF are recorded since the beginning of the expansion of the first American civilizations, especially in Mesoamerica, with an expressive vegetation suppression and fragmentation both of which were much intensified after the arrival of the Europeans at the Neotropics [14]. Nonetheless, both deforestation and fragmentation rates were never as high as they are in this millennium (**Figure 1**), particularly following the advance of the agricultural frontiers [3]. This is a worrying scenario whether C sequestration is considered, since a third of the whole global C sink capacity is attributed to well-preserved NF [45]. In addition, this potential has been decreasing, as stated for Amazonian intact forests, which showed the C sink capacity reduced in a third during the millennia transition [43]. The decrease is even sharper in sites where standing forests are managed, for example for timber extraction, both directly because of massive withdraw of hard-wood tress and indirectly because the process leads to loss of seed matrices [3]. For instance, average biomass accumulation rates in logged areas of Amazonia were lower than a half in comparison to areas under natural regeneration in the same region [48]. Fortunately, areas of fast-growing secondary forests are becoming widespread, both across established forests and at their neighborhoods, with a trend of becoming more important in the upcoming sceneries [53]. Then, from the point of view of integrity, NFs are currently a dynamic mosaic of successional phases, where continuous areas with intact vegetation are decreasing, while both fragmentation and natural or controlled regeneration are increasing (**Figure 1**).

Since forest resilience can be expressed in terms of floristic, functional, and biomass dynamics, isolation of areas leads to severe impacts, such as biodiversity loss and reduced C sink capacity [8]. Deforestation and/or fragmentation promote the largely studied edge effects, whose impacts affect the forest interior up to tens to thousands of meters, as does the so-called "vegetation breeze," widely registered for Amazonian forests [54]. This phenomenon is a result of the difference between microclimates of forests and nonforest areas, which leads forest environments to varied levels of desiccation. In this way, the drier and warmer the

adjacent area, the more impactful is the disturbance, with areas under regeneration, then, playing an important role in mitigating the process. Additional edge effects are noted when forest suppression is combined with fire occurrences [55]. In these cases, atmospheric water droplets may be condensed to aerosol particles, which hamper the formation of proper water drops, intensifying the dryness in the region. Perhaps the most immediate outcome of this whole process is biodiversity loss, with even the most diverse fragments showing significant decrease of abundance/diversity of both fauna and nonarboreal plants, such as lianas and epiphytes [34]. Likewise, only large fragments may harbor plants that require a large area or specific habitats, which, however, does not mean that small forest patches have no ecological importance [33, 54]. In fact, isolation of fragments hampers biodiversity conservation and functional dynamics maintenance, and, because of this, all fragments may have an important role both as eventual reservoirs for plant species and as stepping stones for fauna, processes which are more effective at shorter distances from well-conserved forest remains [34, 53].

Climatic traits are also important modulators of forest resilience (see sessions IV and VI), since they strongly control physiologic traits, which, in their turn, are responsible for controlling individual processes, with important ecological implications, such as tree growth and mortality [8]. Physiologic responses leading to mortality include both increases on photorespiration oxidative stress and C starvation and hydraulic failure, all of them directly or indirectly linked to reduced differences between soil and leaves hydric potentials [56]. Despite the experimental difficulty for studies on the theme, many inferences have been done, especially for the better-studied Amazonian forests. For instance, biophysical processes, such as mechanical and hydraulic failure, have been claimed as the main inducers of large-trees mortality in Amazonia during the last 30 years, together with their accelerated growth in response to CO_2-fertilization [43]. Such increased growth would be linked to the ability of plants under higher concentration of atmospheric C to maintain their stomata closed during a longer period and, in this way, avoid desiccation [54]. Nevertheless, this mitigation mechanism might not avoid increases on embolism occurrences, since acquisitive water use strategies of RF usually include cheap transport throughout larger vases and leaves lacking very negative hydric potential [56]. On the other hand, ecophysiologic responses may also mitigate oxidative stress, as it was claimed for Amazonian forests, where increased emissions of biogenic volatile organic compounds, such as isoprene, in response to warmer temperatures, should have led to reduced tree mortality rates [49]. Regarding drought and DF species, the ability of controlling C absorption would favor functional groups in different ways. Deciduous species would be more competitive under intensified and short dryness, while the evergreens would show lower mortality rates under prolonged but weak droughts because they can control stomatal opening and avoid C starvation [51].

Intensified dryness as an effect of less and/or more variable rainfall are expected to be the worst outcome of the predicted climatic changes for both biomass and community dynamics in NF, since increases in temperature were not correlated to biodiversity losses during the former global warming [19]. However, warming and more severe droughts are already in course, with field observations, most of them for RF (see sessions IV and VI) confirming that forest resilience is indeed correlated with water availability. In spite of the lack of information for other forests, experimental data for the Amazonian show that their resilience can be high, since most of species can stand until 60% of soil hydric content losses and significantly

maintain their survival rates [19]. It is not known, for example, whether SDF species will survive under new climatic conditions at their own current geographic location, since these can become very harsh and perhaps incurring in the desertification of those regions [57]. Likewise, some authors believe that changes in climatic traits in some RF regions, such as eastern Amazonia, will both disturb the stability of the local community and favor the arrival of SDF/savanna species, depending on soil fertility and fire frequency and intensity [51], while others claim that warmer temperatures will lead to increased mortality at high altitudes and boost the relative abundances of lowland tropical species [49]. Anyway, dispersal is a potential limiting for species migration across the Neotropics, since both defaunation and fragmentation are in course processes under accelerated rates.

Notwithstanding, continued alterations in both species distribution and functional composition are expected for NF up to the end of this century. Such alterations are likely to result in reduced carbon storage, as observed for Amazonia, while some authors believe that resilience of natural or man-induced secondary regeneration will decrease (see session VI) [51]. One reason, with an optimistic hope, from the point of view of C sequestration, perhaps that the vegetation cover of regions currently harboring RF will change to SDF, while the opposite will not happen. As SDF species are slow growing, which may be even accentuated under drier conditions, rates of C sink would decrease in all regions. The application of climatic projections to predict future species range is usual, but it is not an easy work predicting changes in community composition and forest structure, from which C dynamics is calculated [58]. Then, computer simulations for NF biomass and floristic dynamics show divergent results, sometimes confirming the above-cited scenarios. For example, tropical NF will have the floristics highly affected during the next decades, with the mortality of big trees responding for almost 30% of AGB loss, while lowland Amazonian forests will be partially replaced probably by SDF or, less likely, by savannas [23]. Meanwhile, secondary lowland NF will provide a large C sequestration for the next 40 years, equivalent to all the C emissions by the whole Neotropics during the last two decades [47] (**Figure 3**), perhaps favored by CO_2-fertilization, which combined with the reduction of the current levels of deforestation, would lead Amazonian forests' structure to remain almost intact even if atmospheric CO_2 levels are double the present [54]. The larger consensus among researchers, however, is that the more information such models incorporate as independent variables, the more trustworthy will be the simulated NF responses to climate changes [49, 58]. In this way, models should incorporate answers for some basic questions [49, 53]: (a) which will be the forest types more affect by dryness and how will they be affected? (b) how will fauna (dispersers, predators, etc) distribution be affected? (c) which plant physiologic traits will enhance or mitigate both dispersal and mortality under the new scenarios? (d) why are both large and small trees affected in different ways by drought? (e) how different species are affected by the all these processes?, and (f) in which ways does secondary forests growth affect the neighbor environmental conditions?

Some of those questions, or at least part of them, are already being answered, for example, how shifts in tree community composition lead to alterations of both fungal diversity and the linked vegetation drought resistance [23]. Others, such as arboreal community vigor during seasonal or eventual dryness, may be correlated to remote-sense observational data, which could easily be incorporated as independent variables in models [49]. Additional predictors to be incorporated are described in the sessions IV and VI of this chapter, including how

Figure 3. Estimated C sequestration by lowland Neotropical secondary forests (<1000 m), as stated by Chazdon et al. (2016) [47].

fragmentation modulates the neighboring forest environments as a response of vegetation breeze, as well as which is the correlation of logging intensity and biomass recovering over-time, and how floristics dynamics are affected by drought. Most of these studies, however, were settled in Amazonian forests, remaining a huge lack of information for the other RF and all SDF [51], with the exception of the environmental traits modulating floristics, which are available for most NF (session IV). In this way, our knowledge regarding the future changes on NF carbon storage leading to a carbon-cycle feedback is still largely uncertain [58]. Thus, if we want to improve such predictions, urgent goals need to be set, such as expanding the existing information for the all NF types and also investigating other theories, as those exemplified in the first paragraph of this session, which requires massive investments in long-term observations and experiments on the ground across the whole Neotropics.

8. Conclusions

The potential major role of NF for mitigating the increased levels of anthropogenic atmospheric carbon dioxide is undebatable. Despite the few certainties about their ecological responses facing global climatic changes, it is vital to use the current knowledge to both conserving and recovering those forests. Survival of such invaluable forests, from the point of view of biodiversity maintenance and/or C sink, is directly dependent on decreasing deforestation rates. Forest suppression is already inducing expressive impacts such as the increase of 1 month on dry season at the arc-of-deforestation, already observed, and the expected severe disturbs on the neighboring south-eastern Amazonia, both on vegetation and hydrology [55]. Forests historically more disturbed may even disappear under continued deforestation, as claimed for the much endangered SDF in both the Caatinga and Cerrado domains [36, 59]. Ironically, if SDFs

were widely distributed across the Dry Diagonal during the drier periods of the Pleistocene, it is likely that water-conservative species of these domains should also survive under the supposed dryer future conditions in their neighboring regions and work as biological sources for their colonization. Considering a scenario of no anthropic intervention for decreasing SDF high fragmentation, migration across lands would be very unlikely to occur, while surviving riverine SDF would adopt a major role in such dispersal-dependent processes. Likewise, a second but not less important role for this corridor vegetation is that of a species reservoir, which would be also the case of the western Amazonia, and all other RFs under maritime moisture influence.

Improving both cover extent and biodiversity/biomass is also of central importance for the maintenance of forest environmental services. Some regions deserve special attention, as exemplified by both the ecotonal areas with drier domains, and wide and well-conserved old forests borders. In such places, reforestation should be massive, while within the domains, at least the number of stepping stones should be increased. Active intervention may be required for secondary forests according to their conservation goals [53], such as the introduction of late-successional species in isolated fragments with the objective of C sequestration and/or biodiversity conservation. Likewise, reduced moist areas would be the most appropriate sites for the establishment of managed-logging stands, which should be done under serious criteria, and preferentially surrounding existing forests, aiming at the conservation of their environmental traits.

9. Final considerations

In a general manner, it is very unlikely that NF will conserve their historical ecosystems and hold the prevalent past environmental and biota proprieties [60]. Instead, the replacement of those forests for either hybrid or novel ecosystems is more likely. However, environmental services such as nutrient, including C, cycling rates, do not necessarily have to change, but if we want to avoid this, prompt habit changes are need. Poor logging practices, forest suppression, and extensive monocultures are just few examples of the unhealth human relationship with nature. On the other hand, forest management practices already in course in many sites must be expanded to the whole Neotropics. Some of those recovering forests not only harbor a great biodiversity, for example those in the Atlantic domain [53], but also sink considerable C amounts (**Figure 3**). Anyway, the major forest regrowth polices worldwide always included both economic incentives and law enforcement, and the improvement of both practices is welcomed in the Neotropics, whether an environmental collapse is not desired

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