ECOLOGY

Strong floristic distinctiveness across Neotropical successional forests

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Forests that regrow naturally on abandoned fields are important for restoring biodiversity and ecosystem services, but can they also preserve the distinct regional tree floras? Using the floristic composition of 1215 early successional forests (≤20 years) in 75 human-modified landscapes across the Neotropic realm, we identified 14 distinct floristic groups, with a between-group dissimilarity of 0.97. Floristic groups were associated with location, bioregions, soil pH, temperature seasonality, and water availability. Hence, there is large continental-scale variation in the species composition of early successional forests, which is mainly associated with biogeographic and environmental factors but not with human disturbance indicators. This floristic distinctiveness is partially driven by regionally restricted species belonging to widespread genera. Early secondary forests contribute therefore to restoring and conserving the distinctiveness of bioregions across the Neotropical realm, and forest restoration initiatives should use local species to assure that these distinct floras are maintained.

INTRODUCTION

Successional forests cover nearly 30% of the Neotropics and are expanding (*1*). These naturally regenerating forests are increasingly important for climate change mitigation (*1*) and for the restoration of biodiversity and ecosystem services in human-modified landscapes (*2*). Although these secondary forests harbor high species diversity, they contain only a subset of species from the regional species pool (*2*). Whether these secondary forests can help preserve the distinctiveness of Neotropical bioregions (*3*) remains unknown.

Neotropical forests are the most species-rich forests in the world because of a mixing of North and South American biotas (*4*), and the intense biotic interchange between drier and wetter environments over evolutionary history (*5*). These interchanges—combined with processes of vicariance, speciation, long-distance dispersal, migration, and environmental filtering—have shaped the current species composition of Neotropical forests and its distinctive biogeographic regions (*6*, *7*). Species exchange, dispersal, and migration across the Americas have been limited by the large continental distances and by orographic and climatic barriers that emerged in different moments in time. About 3 million years (Ma) ago, the North and South American continents were connected by the Panama Isthmus, intensifying species exchange. Important biogeographical barriers for forest species are the dry diagonal in South America, a region that has experienced a relatively stable arid climate since the Eocene (ca. 33 to 38 Ma), and the uplift of the Northern Andes along with the formation of associated dry environments (ca. 34 to 4 Ma) (*8*, *9*).

In addition, environmental filtering imposed by Pleistocene climate variations (ca. 2.6 Ma to 11,000 years) and present climatic and edaphic conditions constrain the establishment of new species, contributing to distinctive species assemblages within the continents (*6*, *10*, *11*). Climatic seasonality has been suggested to be the most important environmental condition defining the main boundaries of Neotropical bioregions (*6*), the floristic distinctions between neighboring evergreen, deciduous and semideciduous forests (*12*, *13*), and the dominant functional traits of moist forests (*14*). Biogeographical patterns in floristic variation have been documented for old-growth forests (*15*–*18*), but not for the subset of species that colonize successional forests in human-modified landscapes across the Neotropics.

Along with historical and ecological processes, humans transformed Neotropical ecosystems in the past ca. 10,000 years and strongly influenced their species composition through the intentional or unintentional spread of some species and elimination of others (*19*, *20*). Species with fruits used by humans have been spread outside their natural distribution range (*19*), like cocoa (*Theobroma cacao*) that originated in the Amazon and was largely cultivated in Mesoamerica in pre-Columbian times. Disturbance-adapted species might have been unintentionally favored by the different cycles of forest opening and regrowth over time. Indigenous people opened large tracts of forest landscapes to allow human settlements and agricultural fields, more intensively in Mesoamerica. Upon European arrival, the extermination of indigenous people led to the regrowth of 55.8 Mha of forests across the continents (*21*), expanding the area that could be colonized by early successional species. These regrowing forests were partially cleared again to give place to croplands and pastures, whose area expanded exponentially from the 17th century onward (*22*), with the fastest conversion rates during the 20th century (*23*, *24*). Landscapes have been since reconfigured by shifting

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cultivation, land-use conversion, fires, and forest exploitation, leading to further reduction of old-growth forest area (*19*, *23*, *24*) and expansion of habitats favorable to disturbance-dependent early successional species. These transformations may also disfavor forest-dependent late successional species, creating landscapes dominated by early successional ones (*25*).

The combination of the expanding extent of regrowth with the reproductive and growth strategies of early successional species may increase their chances of getting dispersed across the continents (*26*). Early successional species have fast growth rates and short life cycles, and produce large amounts of seeds within a few years after establishment. Most of these species produce small seeds dispersed by wind or by generalist frugivores (*27*), allowing them to be dispersed easily and potentially over longer distances and across biogeographic barriers. Most of these seeds exhibit dormancy, which allows survival under adverse conditions (*28*). Over evolutionary history, these traits might have allowed early successional taxa to migrate across the continents and then speciate by vicariance when geographical or climatic barriers formed, or radiate following the development of adaptations to contrasting environmental conditions (*29*). Both possibilities would contribute to distinct species composition across the continents. The widespread pioneer genus *Cecropia*, for example, expanded its distribution range because of long-distance dispersal events (*26*) and spread over the Neotropics before the onset of the Andean uplift, after which it radiated into more than 60 species with varying distribution ranges (*30*). Nevertheless, if dispersal events are recent and/or mediated by humans, there might not be enough time for speciation and the same species would be found repeatedly across the Neotropical realm. *Guazuma ulmifolia*, for example, is commonly found regenerating in pastures across Neotropical regions and over a wide range of environmental conditions (*31*). Rapid and recent dispersal could result in secondary forests with similar floristic composition across the Americas, undermining the continental-scale diversity of Neotropical floras.

To elucidate the patterns of floristic differentiation across Neotropical successional forests, we address these questions: (i) How distinct are early successional assemblages across the Neotropics, how many floristic groups do they form, and where are they situated? (ii) How are geographical, environmental, and anthropogenic factors associated with these early successional floristic groups? We hypothesized that if anthropogenic transformations have expanded the geographical ranges of early successional species, we would find strong similarities in species composition across the Neotropics. These floristic groups would be associated with anthropogenic and environmental factors and should cover large areas, because both long-distance dispersal traits and anthropogenic-driven expansion of favorable habitats would have obscured the signal of biogeographic history but not of environmental filtering. Processes occurring at different time scales, mediated by environmental filtering, dispersal limitation, and anthropogenic transformations, may define the current floristic composition of successional forests. Therefore, we explore the floristic dissimilarity at genus and species level to get insights into the underlying processes of floristic differentiation.

We used the largest database of lowland tropical secondary forests (2ndFOR) based on 1215 plot surveys and 102,834 trees to characterize the genus and species composition of 75 human-modified landscapes across dry, seasonally dry, moist, and wet Neotropical forests. Each landscape is composed of multiple secondary forests with time since abandonment ranging from 1 to 20 years, which is the most common age range in the Neotropics (*1*). Thus, these landscapes encompass the set of species found in chronosequences spanning 20 years of succession. We calculated the floristic dissimilarity of the 75 landscapes using the Simpson dissimilarity index applied separately to species and genus occurrence. Landscapes were then clustered on the basis of their dissimilarity using the unweighted pair group method with arithmetic mean (UPGMA). We described the taxonomic composition of clusters focusing on the widespread genera and species. Next, we used a machine learning approach to identify how environmental factors (climatic and edaphic conditions), anthropogenic impacts (previous land-use history, forest cover, and human footprint), and geographical location (related to dispersal limitation) are associated with the floristic groups. Last, we discuss the implications of our findings for restoring and preserving Neotropical bioregions.

RESULTS

Early successional floristic groups

The young successional forests had 2164 species and 680 genera. Landscapes across the Neotropics showed high floristic dissimilarity in species composition (mean ± SD: 0.90 ± 0.12) and genus composition (0.72 ± 0.17). The clustering of landscapes based on their genera and species composition is explored at two levels of explained dissimilarity: Higher-level clusters (hereafter "clusters") that explain around 60% of the floristic variation are further split into lower-level clusters (hereafter "groups") that explain 90% of the variation (figs. S2 and S5). We explore the higher-level clusters because at around 60% of dissimilarity explained, a small number of clusters explain a large proportion of the dissimilarity (figs. S2 and S5). Clustering based on genus composition resulted in four higher-level clusters explaining 67% of floristic variation and 18 lower-level groups explaining 91% of floristic variation (figs. S4 to S6). Clusters defined on the basis of genus and species composition were consistent with a supplementary network analysis (Supplementary Text and figs. S12 and S13).

A considerable proportion of the floristic variation at the species level (66%; fig. S2) was explained by four higher-level clusters that separated the early successional communities into Dry Forest cluster, Southern South America, Equatorial Moist Forests, and Middle America (Fig. 1A and fig. S1). The Dry Forest cluster contains a single landscape located within the Caatinga biome, and had the most distinctive floristic composition, forming the first split, which explains 3% of the total variation in the data. The second node separates Southern South America, which includes semideciduous forests and moist subtropical Atlantic forests (explaining 27% of the dissimilarity). Last, the moist and wet forests of Equatorial Moist Forests were separated from the Middle America cluster, which includes dry, moist, and wet forests (explaining an additional 39% of the dissimilarity in the data; fig. S2). Between-group dissimilarity (mean, 0.97) was significantly higher than within-group dissimilarity (mean, 0.81) [analysis of similarities (ANOSIM) $P = 0.001$, $R = 0.72$; the ANOSIM statistic R varies from 0 to 1, with higher values indicating higher between-group dissimilarities (*32*)]. The Middle America cluster includes large floristic variation despite the smaller area covered by it (fig. S3).

A total of 14 lower-level floristic groups were needed to explain 90% of the floristic dissimilarity of species across landscapes

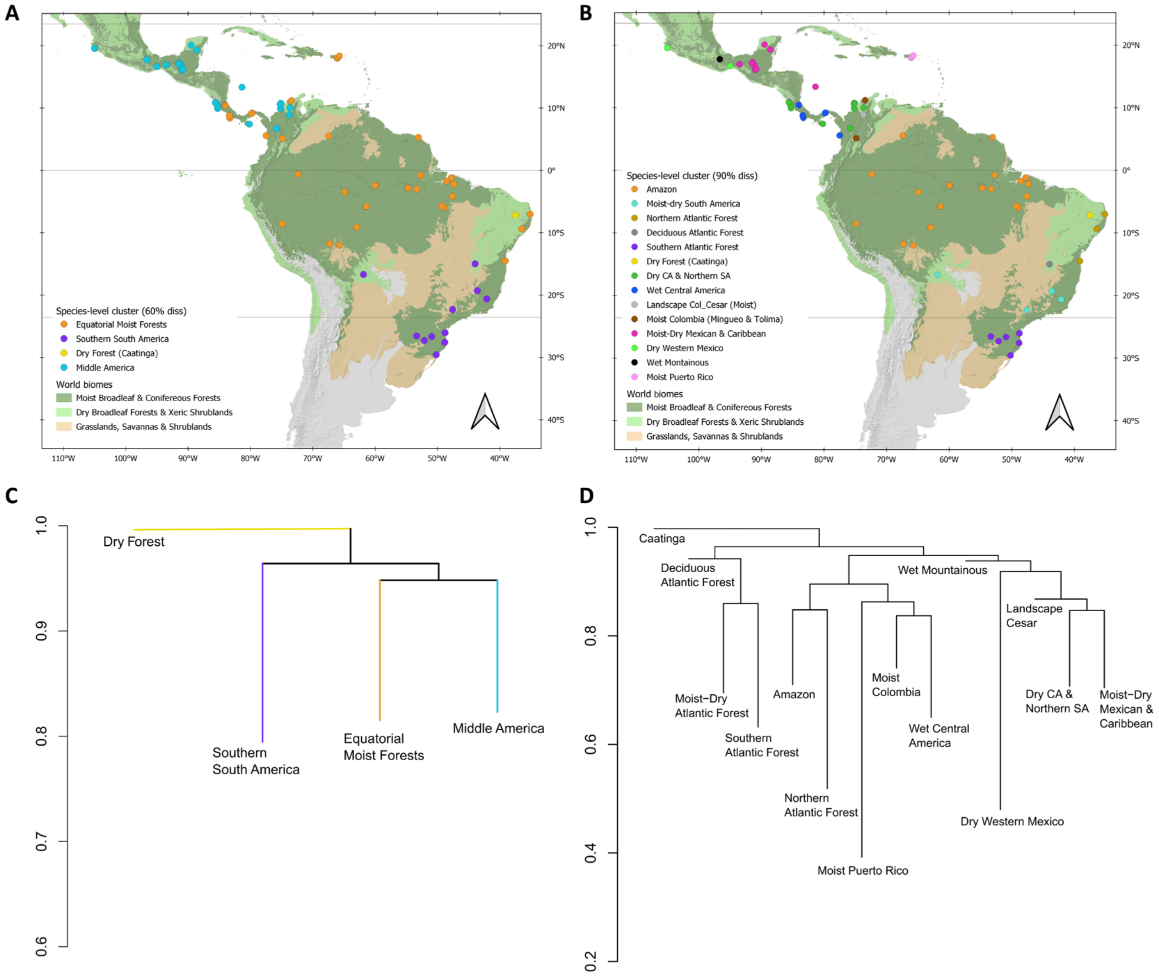

Fig. 1. Clustering of landscapes based on the species composition of early successional communities. (**A**) Higher-level clusters (four floristic groups) explaining 60% of the variation in floristic species composition. (**B**) Lower-level groups explaining 90% of the variation in floristic species composition (14 floristic groups). The location of moist and dry forests as well as the two major biogeographical barriers [the Andes at the northwest of South America and the dry savannas (beige background)] are shown in (A) and (B). For each cluster level, the dendrogram provided shows the mean Simpson dissimilarity values and relationships among the four higher-level clusters (**C**) and among the 14 lower-level groups (**D**). Please note different scales of Simpson dissimilarity in (C) and (D). The consensus cluster with landscapes as tips is provided in fig. S1. CA, Central America; SA, South America.

(Fig. 1, B and D, and fig. S1). Ten groups contained multiple landscapes, whereas four groups were made of single landscapes, such as the Dry Forest cluster that only contains one Landscape representing the Caatinga biome. The Southern South America cluster was divided into three groups: Deciduous Atlantic Forest, Moist-Dry South America, and Southern Atlantic Forest. The Equatorial Moist Forest cluster was divided into five groups: Wet Central America, Moist Colombia, Amazon forest, Moist North Atlantic Forest, and Moist Puerto Rico. Last, the smaller land area of Middle America cluster was divided into five floristic groups: Dry Western Mexico, Moist-Dry Mexico & Caribbean, Dry Central America & Northern South America, and two locally occurring groups—the Wet Mountainous group (composed by a landscape within the Mexican Chinantla region) and the Landscape Cesar (which is a moist forest in Northern Colombia) (Fig. 1B). Between-group dissimilarity (0.93) was significantly higher than within-group dissimilarity (mean, 0.69), supporting the floristic groups (ANOSIM $P = 0.001$, $R = 0.88$).

Taxonomic composition of floristic groups

Across the 14 lower-level floristic groups, the moist and wet forests of Central America and the Amazon shared more species with other floristic groups than the dry forests and the South Atlantic forests (Fig. 2A). The Dry Forest containing the Caatinga landscape was the most distinctive floristic group, having only one species shared (*Mimosa tenuifolia*) with one other group (Dry Western Mexico) (Fig. 2A). Note that the number of shared species is directly related to the number of landscapes comprised in the floristic groups (fig. S7), as the larger the sample size (in total sampled area or number of landscapes), the higher the number of species sampled and the higher the chance of having a species shared with another floristic group. However, floristic groups with similar sample sizes had very different numbers of shared species (Fig. 2A), providing support for the higher proportion of endemism in dry forests and in South Atlantic forests compared to moist and wet forests (Fig. 2A).

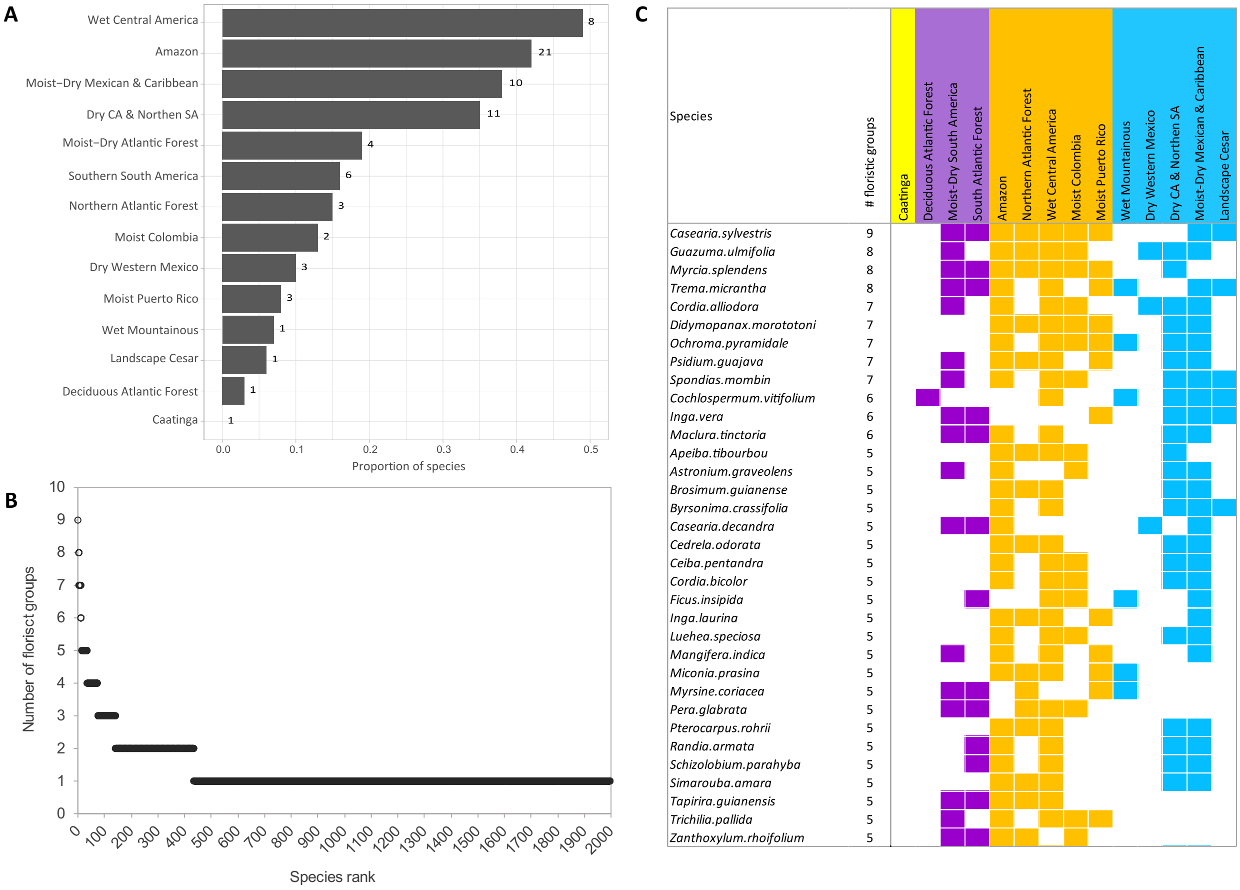

Fig. 2. Species frequency and occurrence across floristic groups. (**A**) Contribution of each floristic group to the species shared across Neotropical early successional communities. The bars show the proportion of species shared between at least two floristic groups (434 species) that occur in a given floristic group. For example, the group Wet Central America contains 47% of the species shared with at least one other group. The number of landscapes included in each floristic group is indicated on the right side of the bars. (**B**) Rank-frequency curve for the 2163 species in the database. (**C**) List of the most widespread species, which occur in five or more floristic groups, and their occurrence in the 14 floristic groups. Species names are ordered according to the number of floristic groups they occur, followed by alphabetic order. Colors refer to the four higher-level floristic clusters in Fig. 1: Dry Forest—Caatinga (yellow), Southern South America (purple), Equatorial Moist Forests (orange), and Middle America (blue).

Most species (1729 species; 80%) were found in only 1 of 14 floristic groups, with only 20% of the species (434 species) found in two or more floristic groups (Fig. 2B). Widespread genera occurring in at least 10 floristic groups were *Cordia* (12 groups) and *Casearia* (11 groups) followed by *Annona*, *Cupania*, *Inga*, *Miconia*, *Ocotea*, *Trichilia*, and *Zanthoxylum* (found in 10 floristic groups; fig. S8). The widespread genera were also the most diverse ones (fig. S8), but the widespread species did not necessarily belong to these large genera. Four widespread species were found in at least eight floristic groups: *Casearia sylvestris* found in nine groups and *Trema micrantha*, *G. ulmifolia*, and *Myrcia splendens* found in eight groups (Fig. 2C). These species occurred most frequently in evergreen and semideciduous forests, and less frequently in dry deciduous forests (Fig. 2C).

Factors associated with floristic clusters and groups

We used a random forest classifier to assess which variables best predict the association of plots to the 14 lower-level floristic groups. The best variables are those that yield more homogeneous groups and higher prediction accuracy and, therefore, when excluded from the analyses, cause a greater decrease in the Gini coefficient and in prediction accuracy (*33*). Analyses based on random forest classifiers showed that floristic variation was significantly associated with geographic location and climatic and edaphic factors, with no significant effect of anthropogenic factors. Higher-level clusters for genus composition were significantly associated with soil pH followed by latitude, longitude followed by temperature seasonality, climatic water deficit (CWD), elevation, and annual precipitation (pseudo-R^2 = 56%; fig. S6C). Soil pH had the highest variable importance because it is consistently higher in drier than wetter forests (table S2), separating the higher-level clusters of Moist Forests and the Dry Forests & Middle America (fig. S6A).

Clustering based on species composition was more strongly associated with geographical location (Fig. 3). The random forest classifier predicted the four higher-level clusters and the 14 species-based floristic groups with low error rates (pseudo-R^2 = 82.0 and 74.0, respectively). Higher-level clusters were significantly associated with latitude, followed by longitude, soil pH, temperature seasonality, CWD, and annual precipitation, in decreasing order of variable importance (Fig. 3A). Lower-level groups were significantly associated with longitude followed by latitude, temperature seasonality, soil pH, soil N, CWD, and annual precipitation (Fig. 3B).

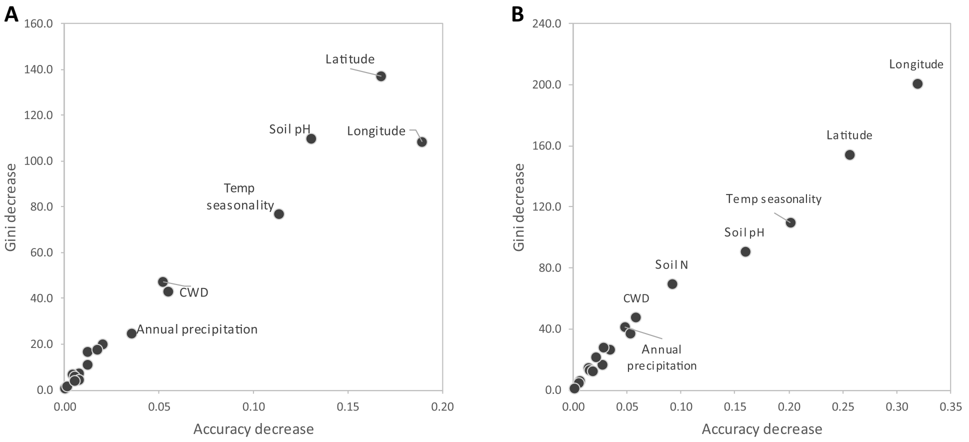

Fig. 3. Relative importance of factors for the classification of floristic groups based on species occurrence. Factors associated with the four higher-level clusters (**A**) and the 14 lower-level groups (**B**). The most important factors for predicting the classification are the ones that yield the largest decrease in Gini coefficient and in accuracy when they are left out of the model. Labels are provided for the significant factors.

Interactions between latitude and longitude as well as between each of them and the other significant factors were among the 30 most frequent interactions in the random forest trees. This means that the splits in random forest trees defined by geographical location (latitude or longitude) were often followed by splits defined by environmental conditions. A complementary random forest analysis including Morrone bioregions as a factor (fig. S9) showed that bioregions became the most important factor associated with species lower-level floristic groups (fig. S10). This is probably because although bioregions are associated to environmental conditions, they additionally include the biogeographic history (e.g., migrations, speciation, extinction, and vicariance processes) (*3*). Together, these results suggest a hierarchical association where floristic groups based on species are first (and strongly) associated with geographic location, potentially as a result of biogeographic history and dispersal limitation, and then with environmental conditions.

DISCUSSION

Early successional communities across the Neotropical realm harbor a large number of species, have high levels of floristic dissimilarity, and form 14 distinctive floristic groups. The clustering of early successional communities at different taxonomic levels suggests a hierarchy of processes governing floristic distinctiveness across the two continents and over evolutionary history. While genus-level composition was strongly associated with environmental conditions (mainly soil pH and mean annual precipitation), clustering at the species level was mainly associated with geographical location and bioregion (fig. S10). Early successional assemblages, therefore, remain strongly dissimilar across the Neotropical realm despite the long-distance dispersal capacity of most pioneer species, their ability to colonize and grow fast, and the human-induced expansion and increase in connectivity of their habitats. Biogeographic history and ecological filtering have been stronger than human transformations in shaping the species composition of secondary forests across the continents.

Despite the ancient anthropogenic influence on Neotropical forests (*20*), and the opening of large tracts of forest intensified in the 20th century (*19*), apparently not enough time has lapsed to exert a substantial influence on the overall floristic distinctiveness across the two continents. However, there is evidence that some species that widely spread across Neotropical secondary forests (Fig. 2C) have been carried around or favored by humans. Examples are the widespread fruits mango (*Mangifera indica*), originally from Asia, and guava (*Psidium guajava*), originally from South America (*34*). Other widespread species such as *C. sylvestris*, *T. micrantha*, and *G. ulmifolia* (Fig. 2C) have broad environmental tolerances, are dispersed by generalist birds, successfully colonize pasturelands (*31*, *35*), and can be locally useful (*20*). The role of humans on the current distribution of such species should be further investigated.

What factors are associated with lower-level floristic groups?

The main factors associated with the 14 floristic groups of species composition were location and climatic and edaphic conditions, similar to patterns found for old-growth forests (*6*, *11*, *36*). Factors related to anthropogenic impact (previous land-use type, landscape forest cover, and human footprint) were not significantly associated with floristic groups. Together, our results indicate that biogeographic history and ecological filtering, rather than anthropogenic impact, drive variation in species composition of early successional forests at the continental scale in the Neotropics.

It is important to note that our dataset is mostly comprised by landscapes with relatively high forest cover (range of 26 to 99%; table S2) and low previous land-use intensity (fig. S2). Degraded landscapes may have lower species diversity and lower floristic dissimilarity because anthropogenic impacts narrow down the subset of species able to establish in secondary forests (*37*–*39*). Nevertheless, secondary forests on highly transformed landscapes have also shown high floristic variation, i.e., high beta-diversity (*40*, *41*), potentially as a result of combinations of stochastic and deterministic processes acting upon the local species pool (*42*). Future studies should include a broad gradient of forest cover and land-use intensity to evaluate whether the floristic distinctiveness of secondary forests is reduced with anthropogenic impact or whether the patterns found here still hold because the successional species are a subset of the local species pool (*2*, *43*).

Geographic location had the highest variable importance for all floristic groups (table S2), suggesting a strong association of the successional flora with biogeographic history and dispersal limitation. Location summarizes multiple spatially structured factors, including environmental conditions and constraints to species dispersal and migration over evolutionary history (*44*, *45*). Although we cannot disentangle the effects of these factors, the strong explanatory power of geography suggests an important effect of dispersal limitation for explaining the variation in the floristic composition of secondary forests at the continental scale. In addition, the high environmental affinity of genus composition (fig. S6) and the restricted distribution of species belonging to widespread genera (fig. S8) suggest that speciation, resulting from dispersal constraints, partially underlies the variation in species composition of successional forests.

After geographical location, temperature seasonality is the most important factor separating multiple floristic regions (table S3), and especially the Southern Atlantic Forests from the rest (Fig. 1, A and B, and table S3). Temperature seasonality increases with latitude and defines bioregion boundaries across the globe, across Neotropical old-growth forests (*46*), and specifically between the Amazon and (sub)tropical Southern Atlantic Forest (*6*, *14*). Southern Neotropical forests have experienced seasonal climates over evolutionary history (*47*), resulting in a tree community with different functional traits than the other moist Neotropical forests (*14*). Low winter temperatures may limit the occurrence of Amazonian species and define the distribution limits of key Southern Atlantic Forest species such as the gymnosperm *Araucaria angustifolia* (Bertol.) Kuntze.

Soil conditions were the next most important factor, with low soil pH separating the weathered acidic soils of the Amazon region and high soil N concentration separating the fertile volcanic soils of Middle America (tables S2 and S3). The low soil pH of the Amazon floristic region (table S2) correlates with low nutrient availability (especially phosphorus), affecting plant species distribution (*48*). Although fertile soils and soils with higher pH are generally associated with drier climates [(*49*); table S2], nitrogen concentration was substantially higher and significantly associated with floristic regions located in Middle America that include dry (Dry Central America & Northern South America), moist (Moist-Dry Mexican & Caribbean, Wet Central America, Moist Puerto Rico), and wet forests (Wet Mountainous) (table S2).

Water availability was less important than soils in defining the floristic groups based on species (Fig. 3), but was important for genus composition (fig. S6, C and D). CWD was an important factor separating the driest forests of the Caatinga and Dry Western Mexico (table S2). These dry forests have the lowest values of annual precipitation (<900 mm) and highest CWD (<−920 mm/year) (table S2). The early successional communities in these regions have a strongly distinct genera and species composition compared to neighboring less-dry, moist, and wet forests (Fig. 1, B and D, and fig. S6), in agreement with the separate phylogenetic origin of dry forests (*13*, *50*) and the high levels of endemism found in the Caatinga (*17*). This supports the idea that a strong deficit in water availability is an important environmental filter defining the floristic composition of deciduous dry forests (*13*), thus restricting the similarity with neighboring less-dry forests (Fig. 1D). Conversely, forests under intermediate climatic conditions may be more likely to exchange species and therefore be more susceptible to biotic homogenization.

Long-term environmental filtering and recent dispersal limitation define floristic variation in early secondary forests

The clustering of early successional communities based on different taxonomic levels suggests a hierarchy of processes governing the floristic distinctiveness across the continents. The floristic variation at the genus level shows a high dispersal capacity across the continents, with higher-level clusters spread over broad latitudinal ranges, and a strong association with environmental conditions of soil pH and temperature seasonality (fig. S6, A and C). The higher- and lower-level floristic clusters based on species, on the other hand, are mainly associated with geographical location (Fig. 3) and bioregions (fig. S10B).

Clustering based on both genus and species agrees on the distinctiveness of the Southern South American cluster (Fig. 1 and fig. S6), suggesting an old radiation of these early successional assemblages and a prevailing effect of temperature seasonality in defining floristic composition (Fig. 3, A and B; fig. S6; and table S3). The other higher-level floristic clusters are associated with soil pH for the genus-level clustering and with geographical location for the species-level clustering. These results corroborate previous findings that phylogenetic turnover is strongly associated with environmental conditions, while species turnover is more related to spatial distance (*15*, *45*, *51*). Combined, these results suggest a key role of environmental filtering in selecting widespread higher-level taxa and of dispersal limitation in contributing to species diversification and ultimately to the high floristic dissimilarity in present-day early secondary forests.

Biogeographic history influences early successional forests

The higher-level clusters based on species composition reflect the biogeographic history of Neotropical flora, agreeing with previous biogeographic evidence of the dry diagonal separating the Southern Atlantic forests (Fig. 1A) (*52*, *53*). The so-called dry diagonal is a large region with relatively stable dry environmental conditions since the Eocene, which is today covered by the Cerrado and Caatinga. The dry diagonal has served as an important biogeographical barrier between the Southern Atlantic Forest and the Amazon throughout the evolutionary history of different taxonomic groups (*52*). This barrier has been less important in its northern portion, where a moist forest corridor has connected the Amazon to the Northern Atlantic Forest region during wetter periods over evolutionary history (*7*). This may explain the higher similarity of genera and species between the early successional communities of the Northern Atlantic Forest and the Amazon (Fig. 1D), agreeing with patterns found in old-growth forest assemblages (*52*, *53*).

The other important distinction, between Equatorial Moist Forests and the floristic group of Middle America, agrees with the different origins of North and South American taxa (*4*, *54*). Lower-level groups for both genus and species composition show a clear distinction between South America and Middle America floristic groups (Fig. 1D), suggesting that the Andes had acted as a major barrier restricting species exchange and delimitating bioregions (*3*, *17*). Moist and dry forests of Northern South America are more similar to those of Central and Middle America than to those of Amazonian or Atlantic forest groups (Fig. 1D). Although some species, usually the most locally abundant ones, are able to cross over the mountain range (*7*), overall early successional assemblages remain rather divergent. Moreover, the lower-level floristic groups of secondary forests identified here agree with the Neotropical bioregions proposed by Morrone (*3*) (figs. S9 and S10) and mostly coincide with floristic groups identified for lowland forest tree communities (*16*). Using a unique dataset on the species composition of successional forests, we show that present-day early successional communities still maintain the biogeographic signature of Neotropical floras.

Implications for forest restoration

Our results indicate that forests that regrow naturally on abandoned agricultural fields can contribute to the restoration and conservation of distinct Neotropical bioregions. Active restoration projects that plant or favor species outside their natural ranges can reduce these broad-scale diversity patterns and contribute to homogenization. For example, species belonging to the same genus may thrive under similar environmental conditions but in different regions (fig. S7). Typical pioneer genera like *Miconia* and *Inga*, for example, are highly diverse (fig. S8), having different species represented in each floristic group. This diversity underlies the distinctiveness of bioregions and should be considered when defining target species in restoration programs. Guaranteeing the regeneration of locally restricted species (especially from these diverse and widespread genera) is therefore crucial for conserving the broad-scale diversity of Neotropical flora.

Despite the many geographically restricted species, there are a few species with broad distributions over seasonally dry to wet climates, like *G. ulmifolia*, *T. micrantha*, *Ochroma pyramidale*, *P. guajava*, and *Cordia alliodora* (Fig. 2C). These species are commonly used in restoration projects, probably because of their tolerance to contrasting environmental conditions. Some of these species are invasive in other continents (e.g., *G. ulmifolia* in India and *P. guajava* in Africa and Oceania) (*55*, *56*) and could become problematic outside of their natural range. Future studies should investigate the natural distribution range of these species, and why they are so successful, to provide guidance for the selection of species for restoration projects aiming for restoring and conserving the local flora.

Last, our analysis has shown that soil pH, temperature, and climatic water availability are strong determinants of species composition of secondary forests. As land use modifies soil conditions and climate change leads to a global increase in temperature and larger variation in water availability (*57*), global changes may induce shifts in species composition, potentially reducing floristic distinctiveness across the continents. Since young secondary forests represent the first step in forest succession and regeneration, this may have large consequences for the functioning of future old-growth forests, potentially leading to biotic homogenization and loss of biodiversity and forest resilience.

MATERIALS AND METHODS

Dataset

Floristic composition of young secondary forests (1 to 20 years after agricultural land use ceased) was described for 75 sites in 10 countries across the Neotropics, ranging from Central Mexico to Southern Brazil and including the Caribbean islands. The Caribbean islands are included here as they have played a key role in bridging the North and South American plates over the geological history of the continents (*4*, *58*). Across sites, annual precipitation varied from 637 to 6387 mm, mean annual temperature from 14.8° to 27.7°C, and soil cation exchange capacity from 7.7 to 35.4 cmol(c)/kg, thus covering a wide range of environmental conditions and forest types (dry, seasonally dry, moist, and wet). Each sample is composed of a chronosequence of secondary forests with different ages. We selected only young secondary forests up to and including 20 years old, because human-modified landscapes are highly dynamic and most secondary forests persist less than 20 years in the landscape (*1*, *59*). We pooled the species lists of each site to represent the species pool during the first 20 years of succession in that particular landscape. Landscape is our sampling unit for the clustering analysis. In total, we sampled 102,834 trees in 1215 plots across 75 landscapes. Inclusion criterion was ≥5 cm stem diameter at 1.3 m height (dbh) in most landscapes, with only six landscapes including only trees with ≥10 cm dbh. Sampled area in each landscape varies between 0.075 and 9.250 ha (1.32 ha, mean ± 1.70 SD; 0.7 ha, median). All landscapes had high sample completeness, suggesting that they include a large proportion of the estimated species pool (*60*). Species coverage, a measure of sample completeness, ranges from 0 to 1 and measures the "proportion of the total number of individuals in a community that belong to the species represented in the sample" (*60*). Sample coverage varied between 0.71 and 1.00 across landscapes (mean ± SD: 0.96 ± 0.04; median: 0.97), confirming that the samples are representative of the species composition of local early secondary forests.

The dataset contained 2306 morphospecies, of which 2163 (94%) were identified to species level and used in the analysis. We followed the classification system of the Angiosperm Phylogeny Group IV (*61*). We corrected misspellings, updated species names, and standardized synonyms across the database using the most recently updated taxonomic resources for the Neotropics such as the ATDN species checklist (*62*), TNRS (version 4.1) (*63*), Tropicos (version 3.2.3) (*64*), and Flora do Brasil 2020 (version from January 2021) (*65*). When accepted species names differed between databases, the name in the most recently updated database prevailed. The complete species checklist of Neotropical secondary forests of the 2ndFOR network is available upon request from the corresponding author.

Clustering of early successional communities

We described species composition based on species occurrences. Species turnover across landscapes was quantified using the Simpson dissimilarity index because it is independent of differences in species richness across landscapes and therefore represents pure species replacement (*66*). The dissimilarity matrix was then used to cluster landscapes using a consensus tree based on UPGMA, implemented in the R package "recluster" (*67*). This approach removes the bias in clustering related to the order of sites in the database and allows the estimation of bootstrap coefficients for node support. By resampling the order of sites in the original dissimilarity matrix, it creates multiple cluster trees that are used to build a consensus tree that is independent of sampling order. The consensus tree was based on 100 trees and included only nodes found with a frequency of ≥50% across trees (0.5 threshold parameter). The final number of clusters used was based on the number of clusters needed to explain most (90%) of the dissimilarity in species composition. To evaluate the consistency of clusters, we tested whether the dissimilarity was higher between clusters than within clusters with an ANOSIM using the vegan package for R. In addition, we conducted a principal coordinates analysis (PCoA) based on the same Simpson dissimilarity index to allow visualization of the floristic distances across clusters (fig. S3). To further explore the floristic patterns and evaluate the drivers of floristic dissimilarity, we followed the same clustering procedure based on the list of genera. Last, to validate the resulting clustering, we performed a network analysis using the modularity method and the spinglass algorithm to identify groups of sites based on their species composition. We used the R packages NetworkToolbox, networktools, and igraph (*68*–*70*). The results of the network analysis and comparison with cluster approach are presented in the Supplementary Text (figs. S12 and S13).

Factors associated with the spatial distribution of early successional communities

To assess how geographic, environmental, and anthropogenic factors are associated with the floristic clusters, we used a random forest classifier (*33*). We applied the random forest algorithm to all 1215 secondary forest plots to make use of more precise predictor information instead of averages over landscapes. The random forest algorithm tested how different variables correctly classify the plots into the predefined floristic groups found for species composition and for genera composition, by randomly selecting a set of variables in each of the 1000 trees built. On the basis of all trees produced, the accuracy of the final random forest model was assessed as the out-of-bag (OOB) error rate subtracted from 100 (pseudo-R^2). The OOB error rate is the percentage of incorrectly classified samples (landscapes) into groups (floristic groups) in an iterative randomized sample selection (OOB sample) (*33*).

Variable importance in the random forest models was verified by the decrease in node impurity (measured by the Gini index), the decrease in accuracy, and its associated significance value (P value). The Gini index measures the mean decrease in node homogeneity when the variable is used. The decrease in accuracy is measured as the OOB error rate when the variable is not used. The higher the values of both measures, the higher the importance of a given variable (*33*).

We compiled 23 variables representing climatic, edaphic, and anthropogenic factors plus latitude and longitude (to account for spatial autocorrelation) and biogeographic regions [provinces proposed by Morrone (*3*, *71*)]. Climatic variables included in the analyses were the aridity index (*72*), CWD (*73*), mean annual temperature, temperature seasonality, annual precipitation and precipitation seasonality, precipitation in the warmer quarter of the year, and temperature in the driest quarter of the year from the Chelsa bioclimatic variables database (*74*). Edaphic variables were soil bulk density; cation exchange capacity; clay, silt, and sand content; nitrogen content; pH; and organic carbon density from the SoilGrids database (*75*). Topography was represented by elevation and slope from the U.S. Geological Survey global multiresolution terrain elevation data version 2010 (*76*). Anthropogenic impact was represented by the accumulated human footprint in the year 2009 (*77*), the human modification index (*78*), previous land-use history, and forest cover in the surrounding landscape. Previous land-use history was represented by five categories, according to information acquired by the sites' research teams: clear cut (clear cut and burned but not cultivated), shifting cultivation (small-scale swidden-fallow agriculture), pasture (low-intensity cattle ranching), shifting cultivation and pasture (over the land-use period, both systems were applied), and high-intensity land use (conventional agriculture or pasture with use of machinery). The percentage of forest cover in the landscape was estimated within a 5-km buffer around each plot [buffer radii defined as suggested in (*79*)]. Forest cover maps were derived from the Copernicus Global Land Cover Layer collection 3 (*80*). Last, the plot successional age was expressed as the number of years since management had ceased. Plot age was acquired through interviews with land owners and/or through remote sensing by the local team. All variables but successional age, previous land-use history, and forest cover were extracted from the spatial databases using a 100-m buffer around the centroid of each plot.

Before analysis, we applied a variable selection procedure to reduce the number of variables to avoid model overfitting and the selection of spurious variables during permutation. We first preserved only variables that had correlation coefficients lower than ca. 0.70, with most values being lower than 0.5 (fig. S11). Second, we ranked the variables based on their variable importance score (VI) calculated on the basis of permutation and eliminated unimportant variables, which had average VI values lower than the threshold [for threshold calculations, see (*81*)]. Next, variables were sequentially included in the random forest models, and model OOB error rates were calculated. Selected variables were the ones with the highest VI and leading to higher model accuracy (based on OOB error). Variable selection was done using the VSURF R package (*82*). All analyses were done using R version 4.0 (*83*). The final variables used in the analyses are listed in table S2.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at https://science.org/doi/10.1126/sciadv.abn1767

View/request a protocol for this paper from *Bio-protocol*.

REFERENCES AND NOTES

1. R. L. Chazdon, E. N. Broadbent, D. M. A. Rozendaal, F. Bongers, A. M. A. Zambrano, T. M. Aide, P. Balvanera, J. M. Becknell, V. Boukili, P. H. S. Brancalion, D. Craven, J. S. Almeida-Cortez, G. A. L. Cabral, B. de Jong, J. S. Denslow, D. H. Dent, S. J. DeWalt, J. M. Dupuy, S. M. Durán, M. M. Espírito-Santo, M. C. Fandino, R. G. César, J. S. Hall, J. L. Hernández-Stefanoni, C. C. Jakovac, A. B. Junqueira, D. Kennard, S. G. Letcher, M. Lohbeck, M. Martínez-Ramos, P. Massoca, J. A. Meave, R. Mesquita, F. Mora, R. Muñoz, R. Muscarella, Y. R. F. Nunes, S. Ochoa-Gaona, E. Orihuela-Belmonte, M. Peña-Claros, E. A. Pérez-García, D. Piotto, J. S. Powers, J. Rodríguez-Velazquez, I. E. Romero-Pérez, J. Ruíz, J. G. Saldarriaga, A. Sanchez-Azofeifa, N. B. Schwartz, M. K. Steininger, N. G. Swenson, M. Uriarte, M. van Breugel, H. van der Wal, M. D. M. Veloso, H. Vester, I. C. G. Vieira, T. V. Bentos, G. B. Williamson, L. Poorter, Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Sci. Adv.* **2**, 988–993 (2016).
2. D. M. A. Rozendaal, F. Bongers, T. M. Aide, E. Alvarez-Dávila, N. Ascarrunz, P. Balvanera, J. M. Becknell, T. V. Bentos, P. H. S. Brancalion, G. A. L. Cabral, S. Calvo-Rodriguez, J. Chave, R. G. César, R. L. Chazdon, R. Condit, J. S. Dallinga, J. S. de Almeida-Cortez, B. de Jong, A. de Oliveira, J. S. Denslow, D. H. Dent, S. J. DeWalt, J. M. Dupuy, S. M. Durán, L. P. Dutrieux, M. M. Espírito-Santo, M. C. Fandino, G. W. W. Fernandes, B. Finegan, H. García, N. Gonzalez, V. G. Moser, J. S. Hall, J. L. Hernández-Stefanoni, S. Hubbell, C. C. Jakovac, A. J. Hernández, A. B. Junqueira, D. Kennard, D. Larpin, S. G. Letcher, J.-C. Licona, E. Lebrija-Trejos, E. Marín-Spiotta, M. Martínez-Ramos, P. E. S. Massoca, J. A. Meave, R. C. G. Mesquita, F. Mora, S. C. Müller, R. Muñoz, S. N. de Oliveira Neto, N. Norden, Y. R. F. Nunes, S. Ochoa-Gaona, E. Ortiz-Malavassi, R. Ostertag, M. Peña-Claros, E. A. Pérez-García, D. Piotto, J. S. Powers, J. Aguilar-Cano, S. Rodriguez-Buritica, J. Rodríguez-Velázquez, M. A. Romero-Romero, J. Ruíz, A. Sanchez-Azofeifa, A. S. de Almeida, W. L. Silver, N. B. Schwartz, W. W. Thomas, M. Toledo, M. Uriarte, E. V. de Sá Sampaio, M. van Breugel, H. van der Wal, S. V. Martins, M. D. M. Veloso, H. F. M. Vester, A. Vicentini, I. C. G. Vieira, P. Villa, G. B. Williamson, K. J. Zanini, J. Zimmerman, L. Poorter, Biodiversity recovery of Neotropical secondary forests. *Sci. Adv.* **5**, eaau3114 (2019).
3. J. J. Morrone, Biogeographical regionalisation of the Neotropical region. *Zootaxa* **3782**, 1–110 (2014).
4. A. H. Gentry, Neotropical floristic diversity: Phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Ann. Mo. Bot. Gard.* **69**, 557–593 (1982).

5. A. Antonelli, A. Zizka, F. A. Carvalho, R. Scharn, C. D. Bacon, D. Silvestro, F. L. Condamine, Amazonia is the primary source of Neotropical biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 6034–6039 (2018).
6. G. F. Ficetola, F. Mazel, W. Thuiller, Global determinants of zoogeographical boundaries. *Nat. Ecol. Evol.* **1**, 89 (2017).
7. P. V. A. Fine, L. G. Lohmann, Importance of dispersal in the assembly of the Neotropical biota. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 5829–5831 (2018).
8. C. E. Hughes, R. T. Pennington, A. Antonelli, Neotropical plant evolution: Assembling the big picture. *Bot. J. Linn. Soc.* **171**, 1–18 (2013).
9. O. A. Pérez-Escobar, A. Zizka, M. A. Bermúdez, A. S. Meseguer, F. L. Condamine, C. Hoorn, H. Hooghiemstra, Y. Pu, D. Bogarín, L. M. Boschman, R. T. Pennington, A. Antonelli, G. Chomicki, The Andes through time: Evolution and distribution of Andean floras. *Trends Plant Sci.* **27**, 364–378 (2022).
10. A. Esquivel-Muelbert, T. R. Baker, K. G. Dexter, S. L. Lewis, H. ter Steege, G. Lopez-Gonzalez, A. M. Mendoza, R. Brienen, T. R. Feldpausch, N. Pitman, A. Alonso, G. van der Heijden, M. Peña-Claros, M. Ahuite, M. Alexiaides, E. Á. Dávila, A. A. Murakami, L. Arroyo, M. Aulestia, H. Balslev, J. Barroso, R. Boot, A. Cano, V. C. Moscoso, J. A. Comiskey, F. Cornejo, F. Dallmeier, D. C. Daly, N. Dávila, J. F. Duivenvoorden, A. J. D. Montoya, T. Erwin, A. Di Fiore, T. Fredericksen, A. Fuentes, R. García-Villacorta, T. Gonzales, J. E. G. Andino, E. N. H. Coronado, I. Huamantupa-Chuquimaco, R. E. M. Jiménez, T. J. Killeen, Y. Malhi, C. Mendoza, H. Mogollón, P. M. Jørgensen, J. C. Montero, B. Mostacedo, W. Nauray, D. Neill, P. N. Vargas, S. Palacios, W. P. Cuenca, N. C. P. Camacho, J. Peacock, J. F. Phillips, G. Pickavance, C. A. Quesada, H. Ramírez-Angulo, Z. Restrepo, C. R. Rodriguez, M. R. Paredes, M. C. Peñuela-Mora, R. Sierra, M. Silveira, P. Stevenson, J. Stropp, J. Terborgh, M. Tirado, M. Toledo, A. Torres-Lezama, M. N. Umaña, L. E. Urrego, R. V. Martinez, L. V. Gamarra, C. I. A. Vela, E. V. Torre, V. Vos, P. von Hildebrand, C. Vriesendorp, O. Wang, K. R. Young, C. E. Zartman, O. L. Phillips, Seasonal drought limits tree species across the Neotropics. *Ecography* **40**, 618–629 (2017).
11. R. A. Segovia, R. T. Pennington, T. R. Baker, F. C. de Souza, D. M. Neves, C. C. Davis, J. J. Armesto, A. T. Olivera-Filho, K. G. Dexter, Freezing and water availability structure the evolutionary diversity of trees across the Americas. *Sci. Adv.* **6**, eaaz5373 (2020).
12. A. Antonelli, Biogeography: Drivers of bioregionalization. *Nat. Ecol. Evol.* **1**, 0114 (2017).
13. K. G. Dexter, R. T. Pennington, A. T. Oliveira-Filho, M. L. Bueno, P. L. S. de Miranda, D. M. Neves, Inserting tropical dry forests into the discussion on biome transitions in the tropics. *Front. Ecol. Evol.* **6**, 1–7 (2018).
14. B. X. Pinho, M. Tabarelli, C. J. F. ter Braak, S. J. Wright, V. Arroyo-Rodríguez, M. Benchimol, B. M. J. Engelbrecht, S. Pierce, P. Hietz, B. A. Santos, C. A. Peres, S. C. Müller, I. J. Wright, F. Bongers, M. Lohbeck, Ü. Niinemets, M. Slot, S. Jansen, D. Jamelli, R. A. F. de Lima, N. Swenson, R. Condit, J. Barlow, F. Slik, M. A. Hernández-Ruedas, G. Mendes, M. Martínez-Ramos, N. Pitman, N. Kraft, N. Garwood, J. E. G. Andino, D. Faria, E. Chacón-Madrigal, E. Mariano-Neto, V. Júnior, J. Kattge, F. P. L. Melo, Functional biogeography of Neotropical moist forests: Trait–climate relationships and assembly patterns of tree communities. *Glob. Ecol. Biogeogr.* **30**, 1430–1446 (2021).
15. D. M. Neves, K. G. Dexter, T. R. Baker, F. Coelho de Souza, A. T. Oliveira-Filho, L. P. Queiroz, H. C. Lima, M. F. Simon, G. P. Lewis, R. A. Segovia, L. Arroyo, C. Reynel, J. L. Marcelo-Peña, I. Huamantupa-Chuquimaco, D. Villarroel, G. A. Parada, A. Daza, R. Linares-Palomino, L. V. Ferreira, R. P. Salomão, G. S. Siqueira, M. T. Nascimento, C. N. Fraga, R. T. Pennington, Evolutionary diversity in tropical tree communities peaks at intermediate precipitation. *Sci. Rep.* **10**, 1188 (2020).
16. M. A. Cupertino-Eisenlohr, A. T. Oliveira-Filho, M. F. Simon, Patterns of variation in tree composition and richness in Neotropical non-flooded evergreen forests. *Appl. Veg. Sci.* **24**, e12522 (2021).
17. DRYFLOR, K. Banda-R, A. Delgado-Salinas, K. G. Dexter, R. Linares-Palomino, A. Oliveira-Filho, D. Prado, M. Pullan, C. Quintana, R. Riina, G. M. Rodríguez M, J. Weintritt, P. Acevedo-Rodriguez, J. Adarve, E. Álvarez, A. Aranguren B, J. C. Arteaga, G. Aymard, A. Castaño, N. Ceballos-Mago, Á. Cogollo, H. Cuadros, F. Delgado, W. Devia, H. Dueñas, L. Fajardo, Á. Fernandez, M. Á. Fernandez, J. Franklin, E. H. Freid, L. A. Galetti, R. Gonto, R. González-M, R. Graveson, E. H. Helmer, Á. Idárraga, R. López, H. Marcano-Vega, O. G. Martínez, H. M. Maturo, M. McDonald, K. McLaren, O. Melo, F. Mijares, V. Mogni, D. Molina, N. Del Pilar Moreno, J. M. Nassar, D. M. Neves, L. J. Oakley, M. Oatham, A. R. Olvera-Luna, F. F. Pezzini, O. J. R. Dominguez, M. E. Ríos, O. Rivera, N. Rodríguez, A. Rojas, T. Särkinen, R. Sánchez, M. Smith, C. Vargas, B. Villanueva, R. T. Pennington, Plant diversity patterns in neotropical dry forests and their conservation implications. *Science* **353**, 1383–1387 (2016).
18. A. T. Oliveira-Filho, K. G. Dexter, R. T. Pennington, M. F. Simon, M. L. Bueno, D. M. Neves, On the floristic identity of Amazonian vegetation types. *Biotropica* **53**, 767–777 (2021).
19. E. C. Ellis, N. Gauthier, K. Klein Goldewijk, R. B. Bird, N. Boivin, S. Díaz, D. Q. Fuller, J. L. Gill, J. O. Kaplan, N. Kingston, H. Locke, C. N. H. McMichael, D. Ranco, T. C. Rick, M. R. Shaw, L. Stephens, J.-C. Svenning, J. E. M. Watson, People have shaped most of terrestrial nature for at least 12,000 years. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2023483118 (2021).
20. C. Levis, F. R. C. Costa, F. Bongers, M. Peña-Claros, C. R. Clement, A. B. Junqueira, E. G. Neves, E. K. Tamanaha, F. O. G. Figueiredo, R. P. Salomão, C. V. Castilho, W. E. Magnusson, O. L. Phillips, J. E. Guevara, D. Sabatier, J.-F. Molino, D. C. López, A. M. Mendoza, N. C. A. Pitman, A. Duque, P. N. Vargas, C. E. Zartman, R. Vasquez, A. Andrade, J. L. Camargo, T. R. Feldpausch, S. G. W. Laurance, W. F. Laurance, T. J. Killeen, H. E. M. Nascimento, J. C. Montero, B. Mostacedo, I. L. Amaral, I. C. G. Vieira, R. Brienen, H. Castellanos, J. Terborgh, M. de Jesus Veiga Carim, J. R. da Silva Guimarães, L. de Souza Coelho, F. D. de Almeida Matos, F. Wittmann, H. F. Mogollón, G. Damasco, N. Dávila, R. García-Villacorta, E. N. H. Coronado, T. Emilio, D. de Andrade Lima Filho, J. Schietti, P. Souza, N. Targhetta, J. A. Comiskey, B. S. Marimon, B.-H. Marimon Jr., D. Neill, A. Alonso, L. Arroyo, F. A. Carvalho, F. C. de Souza, F. Dallmeier, M. P. Pansonato, J. F. Duivenvoorden, P. V. A. Fine, P. R. Stevenson, A. Araujo-Murakami, G. A. Aymard C, C. Baraloto, D. D. do Amaral, J. Engel, T. W. Henkel, P. Maas, P. Petronelli, J. D. C. Revilla, J. Stropp, D. Daly, R. Gribel, M. R. Paredes, M. Silveira, R. Thomas-Caesar, T. R. Baker, N. F. da Silva, L. V. Ferreira, C. A. Peres, M. R. Silman, C. Cerón, F. C. Valverde, A. Di Fiore, E. M. Jimenez, M. C. P. Mora, M. Toledo, E. M. Barbosa, L. C. de M. Bonates, N. C. Arboleda, E. de Sousa Farias, A. Fuentes, J.-L. Guillaumet, P. M. Jørgensen, Y. Malhi, I. P. de Andrade Miranda, J. F. Phillips, A. Prieto, A. Rudas, A. R. Ruschel, N. Silva, P. von Hildebrand, V. A. Vos, E. L. Zent, S. Zent, B. B. L. Cintra, M. T. Nascimento, A. A. Oliveira, H. Ramirez-Angulo, J. F. Ramos, G. Rivas, J. Schöngart, R. Sierra, M. Tirado, G. van der Heijden, E. V. Torre, O. Wang, K. R. Young, C. Baider, A. Cano, W. Farfan-Rios, C. Ferreira, B. Hoffman, C. Mendoza, I. Mesones, A. Torres-Lezama, M. N. U. Medina, T. R. van Andel, D. Villarroel, R. Zagt, M. N. Alexiades, H. Balslev, K. Garcia-Cabrera, T. Gonzales, L. Hernandez, I. Huamantupa-Chuquimaco, A. G. Manzatto, W. Milliken, W. P. Cuenca, S. Pansini, D. Pauletto, F. R. Arevalo, N. F. C. Reis, A. F. Sampaio, L. E. U. Giraldo, E. H. V. Sandoval, L. V. Gamarra, C. I. A. Vela, H. ter Steege, Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science* **355**, 925–931 (2017).
21. A. Koch, C. Brierley, M. M. Maslin, S. L. Lewis, Earth system impacts of the European arrival and great dying in the Americas after 1492. *Quat. Sci. Rev.* **207**, 13–36 (2019).
22. J. Pongratz, C. Reick, T. Raddatz, M. Claussen, A reconstruction of global agricultural areas and land cover for the last millennium. *Global Biogeochem. Cycles* **22**, GB3018 (2008).
23. E. C. Ellis, K. Klein Goldewijk, S. Siebert, D. Lightman, N. Ramankutty, Anthropogenic transformation of the biomes, 1700 to 2000. *Glob. Ecol. Biogeogr.* **19**, 589–606 (2010).
24. K. Klein Goldewijk, A. Beusen, G. van Drecht, M. de Vos, The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Glob. Ecol. Biogeogr.* **20**, 73–86 (2011).
25. J. Barlow, C. A. Peres, Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philos. Trans. R. Soc. B Biol. Sci.* **363**, 1787–1794 (2008).
26. Z. Y. Wu, J. Liu, J. Provan, H. Wang, C. J. Chen, M. W. Cadotte, Y. H. Luo, B. S. Amorim, D. Z. Li, R. I. Milne, Testing Darwin's transoceanic dispersal hypothesis for the inland nettle family (Urticaceae). *Ecol. Lett.* **21**, 1515–1529 (2018).
27. P. H. S. A. Camargo, M. A. Pizo, P. H. S. Brancalion, T. A. Carlo, Fruit traits of pioneer trees structure seed dispersal across distances on tropical deforested landscapes: Implications for restoration. *J. Appl. Ecol.* **57**, 2329–2339 (2020).
28. D. L. Venable, J. S. Brown, The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.* **131**, 360–384 (1988).
29. S. G. Letcher, J. R. Lasky, R. L. Chazdon, N. Norden, S. J. Wright, J. A. Meave, E. A. Pérez-García, R. Muñoz, E. Romero-Pérez, A. Andrade, J. L. Andrade, P. Balvanera, J. M. Becknell, T. V. Bentos, R. Bhaskar, F. Bongers, V. Boukili, P. H. S. Brancalion, R. G. César, D. A. Clark, D. B. Clark, D. Craven, A. DeFrancesco, J. M. Dupuy, B. Finegan, E. González-Jiménez, J. S. Hall, K. E. Harms, J. L. Hernández-Stefanoni, P. Hietz, D. Kennard, T. J. Killeen, S. G. Laurance, E. E. Lebrija-Trejos, M. Lohbeck, M. Martínez-Ramos, P. E. S. Massoca, R. C. G. Mesquita, F. Mora, R. Muscarella, H. Paz, F. Pineda-García, J. S. Powers, R. Quesada-Monge, R. R. Rodrigues, M. E. Sandor, L. Sanaphre-Villanueva, E. Schüller, N. G. Swenson, A. Tauro, M. Uriarte, M. van Breugel, O. Vargas-Ramírez, R. A. G. Viani, A. L. Wendt, G. B. Williamson, Environmental gradients and the evolution of successional habitat specialization: A test case with 14 Neotropical forest sites. *J. Ecol.* **103**, 1276–1290 (2015).
30. P. Franco-Rosselli, C. C. Berg, Distributional patterns of *Cecropia* (Cecropiaceae): A panbiogeographic analysis. *Caldasia* **19**, 285–296 (1997).
31. H. P. Griscom, M. S. Ashton, Restoration of dry tropical forests in Central America: A review of pattern and process. *For. Ecol. Manage.* **261**, 1564–1579 (2011).
32. K. R. CLARKE, Non-parametric multivariate analyses of changes in community structure. *Austral Ecol.* **18**, 117–143 (1993).
33. L. Breiman, Random forests. *Mach. Learn.* **45**, 5–32 (2001).
34. E. Arévalo-marín, A. Casas, L. Landrum, M. P. Shock, H. Alvarado-sizzo, E. Ruiz-sanchez, C. R. Clement, The taming of *Psidium guajava*: Natural and cultural history of a Neotropical fruit. *Front. Plant Sci.* **12**, 714763 (2021).
35. E. R. Hooper, P. Legendre, R. Condit, Factors affecting community composition of forest regeneration in deforested, abandoned land in Panama. *Ecology* **85**, 3313–3326 (2004).

36. M. A. Cupertino-Eisenlohr, P. V. Eisenlohr, L. Barros-Rosa, A. T. de Oliveira-Filho, M. F. Simon, Environmental variables and dispersal barriers explain broad-scale variation in tree species composition across Neotropical non-flooded evergreen forests. *J. Veg. Sci.* **32**, e13026 (2021).
37. C. C. Jakovac, F. Bongers, T. W. Kuyper, R. C. G. Mesquita, M. Peña-Claros, Land use as a filter for species composition in Amazonian secondary forests. *J. Veg. Sci.* **27**, 1104–1116 (2016).
38. B. K. C. Filgueiras, C. A. Peres, F. P. L. Melo, I. R. Leal, M. Tabarelli, Winner–loser species replacements in human-modified landscapes. *Trends Ecol. Evol.* **36**, 545–555 (2021).
39. M. Tabarelli, C. A. Peres, F. P. L. Melo, The "few winners and many losers" paradigm revisited: Emerging prospects for tropical forest biodiversity. *Biol. Conserv.* **155**, 136–140 (2012).
40. R. R. de Castro Solar, J. Barlow, J. Ferreira, E. Berenguer, A. C. Lees, J. R. Thomson, J. Louzada, M. Maués, N. G. Moura, V. H. F. Oliveira, J. C. M. Chaul, J. H. Schoereder, I. C. G. Vieira, R. Mac Nally, T. A. Gardner, How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecol. Lett.* **18**, 1108–1118 (2015).
41. A. B. Hurtado-M, M. Á. Echeverry-Galvis, B. Salgado-Negret, J. C. Muñoz, J. M. Posada, N. Nordern, Little trace of floristic homogenization in peri-urban Andean secondary forests despite high anthropogenic transformation. *J. Ecol.* , 1468–1478 (2021).
42. N. Norden, H. A. Angarita, F. Bongers, M. Martínez-ramos, I. Granzow-de, F. Bongers, M. Martínez-Ramos, I. Granzow-de la Cerda, M. van Breugel, E. Lebrija-Trejos, J. A. Meave, J. Vandermeer, G. B. Williamson, B. Finegan, R. Mesquita, R. L. Chazdon, Successional dynamics in Neotropical forests are as uncertain as they are predictable. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 8013–8018 (2015).
43. N. Norden, R. L. Chazdon, A. Chao, Y. H. Jiang, B. Vílchez-Alvarado, Resilience of tropical rain forests: Tree community reassembly in secondary forests. *Ecol. Lett.* **12**, 385–394 (2009).
44. C. A. Baldeck, R. Tupayachi, F. Sinca, N. Jaramillo, G. P. Asner, Environmental drivers of tree community turnover in western Amazonian forests. *Ecography* **39**, 1089–1099 (2016).
45. J. E. Guevara Andino, N. C. A. Pitman, H. ter Steege, M. Peralvo, C. Cerón, P. V. A. Fine, The contribution of environmental and dispersal filters on phylogenetic and taxonomic beta diversity patterns in Amazonian tree communities. *Oecologia* **196**, 1119–1137 (2021).
46. A. C. Silva, A. F. Souza, Aridity drives plant biogeographical sub regions in the Caatinga, the largest tropical dry forest and woodland block in South America. *PLOS ONE* **13**, e0196130 (2018).
47. A. T. Oliveira-Filho, D. Cardoso, B. D. Schrire, G. P. Lewis, R. T. Pennington, T. J. Brummer, J. Rotella, M. Lavin, Stability structures tropical woody plant diversity more than seasonality: Insights into the ecology of high legume-succulent-plant biodiversity. *South African J. Bot.* **89**, 42–57 (2013).
48. G. Zuquim, F. R. C. Costa, H. Tuomisto, G. M. Moulatlet, F. O. G. Figueiredo, The importance of soils in predicting the future of plant habitat suitability in a tropical forest. *Plant and Soil* **450**, 151–170 (2020).
49. A. H. Gentry, in *Seasonally Dry Tropical Forests*, S. H. Bullock, H. A. Mooney, E. Medina, Eds. (Cambridge Univ. Press, 1995), pp. 146–194.
50. J. W. F. Slik, J. Franklin, V. Arroyo-Rodríguez, R. Field, S. Aguilar, N. Aguirre, J. Ahumada, S.-I. Aiba, L. F. Alves, A. K, A. Avella, F. Mora, G. A. Aymard C, S. Báez, P. Balvanera, M. L. Bastian, J.-F. Bastin, P. J. Bellingham, E. van den Berg, P. da Conceição Bispo, P. Boeckx, K. Boehning-Gaese, F. Bongers, B. Boyle, F. Brambach, F. Q. Brearley, S. Brown, S.-L. Chai, R. L. Chazdon, S. Chen, P. Chhang, G. Chuyong, C. Ewango, I. M. Coronado, J. Cristóbal-Azkarate, H. Culmsee, K. Damas, H. S. Dattaraja, P. Davidar, S. J. De Walt, H. Din, D. R. Drake, A. Duque, G. Durigan, K. Eichhorn, E. S. Eler, T. Enoki, A. Ensslin, A. B. Fandohan, N. Farwig, K. J. Feeley, M. Fischer, O. Forshed, Q. S. Garcia, S. C. Garkoti, T. W. Gillespie, J.-F. Gillet, C. Gonmadje, I. Granzow-de la Cerda, D. M. Griffith, J. Grogan, K. R. Hakeem, D. J. Harris, R. D. Harrison, A. Hector, A. Hemp, J. Homeier, M. S. Hussain, G. Ibarra-Manríquez, I. F. Hanum, N. Imai, P. A. Jansen, C. A. Joly, S. Joseph, K. Kartawinata, E. Kearsley, D. L. Kelly, M. Kessler, T. J. Killeen, R. M. Kooyman, Y. Laumonier, S. G. Laurance, W. F. Laurance, M. J. Lawes, S. G. Letcher, J. Lindsell, J. Lovett, J. Lozada, X. Lu, A. M. Lykke, K. B. Mahmud, N. P. D. Mahayani, A. Mansor, A. R. Marshall, E. H. Martin, D. C. L. Matos, J. A. Meave, F. P. L. Melo, Z. H. A. Mendoza, F. Metali, V. P. Medjibe, J. P. Metzger, T. Metzker, D. Mohandass, M. A. Munguía-Rosas, R. Muñoz, E. Nurtjahy, E. L. de Oliveira, Onrizal, P. Parolin, M. Parren, N. Parthasarathy, E. Paudel, R. Perez, E. A. Pérez-García, U. Pommer, L. Poorter, L. Qie, M. T. F. Piedade, J. R. R. Pinto, A. D. Poulsen, J. R. Poulsen, J. S. Powers, R. C. Prasad, J.-P. Puyravaud, O. Rangel, J. Reitsma, D. S. B. Rocha, S. Rolim, F. Rovero, A. Rozak, K. Ruokolainen, E. Rutishauser, G. Rutten, M. N. M. Said, F. Z. Saiter, P. Saner, B. Santos, J. R. Dos Santos, S. K. Sarker, C. B. Schmitt, J. Schoengart, M. Schulze, D. Sheil, P. Sist, A. F. Souza, W. R. Spironello, T. Sposito, R. Steinmetz, T. Stevart, M. S. Suganuma, R. Sukri, A. Sultana, R. Sukumar, T. Sunderland, Supriyadi, H. S. Suresh, E. Suzuki, M. Tabarelli, J. Tang, E. V. J. Tanner, N. Targhetta, I. Theilade, D. Thomas, J. Timberlake, M. de Morisson Valeriano, J. van Valkenburg, T. Van Do, H. Van Sam, J. H. Vandermeer, H. Verbeeck, O. R. Vetaas, V. Adekunle, S. A. Vieira, C. O. Webb, E. L. Webb, T. Whitfeld, S. Wich, J. Williams, S. Wiser, F. Wittmann, X. Yang, C. Y. A. Yao, S. L. Yap, R. A. Zahawi, R. Zakaria, R. Zang, Phylogenetic classification of the world's tropical forests. *Proc. Natl. Acad. Sci. U.S.A.* **115**, E3067 (2018).
51. O. J. Hardy, P. Couteron, F. Munoz, B. R. Ramesh, R. Pélissier, Phylogenetic turnover in tropical tree communities: Impact of environmental filtering, biogeography and mesoclimatic niche conservatism. *Glob. Ecol. Biogeogr.* **21**, 1007–1016 (2012).
52. R. M. D. Ledo, G. R. Colli, The historical connections between the Amazon and the Atlantic Forest revisited. *J. Biogeogr.* **44**, 2551–2563 (2017).
53. A. M. M. Santos, D. R. Cavalcanti, J. M. C. Da Silva, M. Tabarelli, Biogeographical relationships among tropical forests in north-eastern Brazil. *J. Biogeogr.* **34**, 437–446 (2007).
54. B. G. Holt, J. P. Lessard, M. K. Borregaard, S. A. Fritz, M. B. Araújo, D. Dimitrov, P. H. Fabre, C. H. Graham, G. R. Graves, K. A. Jønsson, D. Nogués-Bravo, Z. Wang, R. J. Whittaker, J. Fjeldså, C. Rahbek, An update of Wallace's zoogeographic regions of the world. *Science* **339**, 74–78 (2013).
55. K. V. Sankaran, A. A. Khuroo, R. Raghavan, S. Molur, B. Kumar, L. J. Wong, S. Pagad, Global Register of Introduced and Invasive Species – India, version 1.5 (2021).
56. ISSG, Global Invasive Species Database (2021); www.iucngisd.org/gisd/species.php?sc=211.
57. IPCC, *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge Univ. Press, Sixth Asse., 2021).
58. G. Ibarra-Manriquez, J. L. Villasenor, R. Duran, J. Meave, Biogeographical analysis of the tree flora of the Yucatan Peninsula. *J. Biogeogr.* **29**, 17–29 (2002).
59. N. Schwartz, T. M. Aide, J. Graesser, H. R. Grau, M. Uriarte, Reversals of reforestation across Latin America limit climate mitigation potential of tropical forests. *Front. For. Glob. Change* **3**, 85 (2020).
60. A. Chao, Y. T. Wang, L. Jost, Entropy and the species accumulation curve: A novel entropy estimator via discovery rates of new species. *Methods Ecol. Evol.* **4**, 1091–1100 (2013).
61. M. W. Chase, M. J. M. Christenhusz, M. F. Fay, J. W. Byng, W. S. Judd, D. E. Soltis, D. J. Mabberley, A. N. Sennikov, P. S. Soltis, P. F. Stevens, An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* **181**, 1–20 (2016).
62. D. Cardoso, T. Särkinen, S. Alexander, A. M. Amorim, V. Bittrich, M. Celis, D. C. Daly, P. Fiaschi, V. A. Funk, L. L. Giacomin, R. Goldenberg, G. Heiden, J. Iganci, C. L. Kelloff, S. Knapp, H. C. De Lima, A. F. P. Machado, R. M. D. Santos, R. Mello-Silva, F. A. Michelangeli, J. Mitchell, P. Moonlight, P. L. R. De Moraes, S. A. Mori, T. S. Nunes, T. D. Pennington, J. R. Pirani, G. T. Prance, L. P. De Queiroz, A. Rapini, R. Riina, C. A. V. Rincon, N. Roque, G. Shimizu, M. Sobral, J. R. Stehmann, W. D. Stevens, C. M. Taylor, M. Trovó, C. Van Den Berg, H. Van Der Werff, P. L. Viana, C. E. Zartman, R. C. Forzza, Amazon plant diversity revealed by a taxonomically verified species list. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 10695–10700 (2017).
63. B. L. Boyle, N. Matasci, D. Mozzherin, T. Rees, G. C. Barbosa, R. Kumar Sajja, B. J. Enquist, The taxonomic name resolution service: An online tool for automated standardization of plant names. *Bot. Inf. Ecol. Netw.* (2021).
64. Missouri Botanical Garden, Tropicos.org; https://tropicos.org.
65. Jardim Botânico do Rio de Janeiro, Flora do Brasil 2020 (2020), p. v393.274; floradobrasil.jbrj.gov.br.
66. A. Baselga, F. Leprieur, Comparing methods to separate components of beta diversity. *Methods Ecol. Evol.* **6**, 1069–1079 (2015).
67. L. Dapporto, M. Ramazzotti, S. Fattorini, G. Talavera, R. Vila, R. L. H. Dennis, Recluster: An unbiased clustering procedure for beta-diversity turnover. *Ecography* **36**, 1070–1075 (2013).
68. G. Csardi, T. Nepusz, The igraph software package for complex network research. *InterJ. Complex Syst.* **1695**, 1–9 (2006).
69. P. Christensen, NetworkToolbox: Methods and measures for brain, cognitive, and psychometric network analysis in R. *R J.* **10**, 422 (2019).
70. P. Jones, Tools for identifying important nodes in networks (2021), p. 26; https://cran.r-project.org/package=networktools.
71. P. Löwenberg-Neto, Neotropical region: A shapefile of Morrone's (2014) biogeographical regionalisation. *Zootaxa* **3802**, 300 (2014).
72. UNEP, FAO, Global map of aridity (1997); https://data.apps.fao.org/map/catalog/srv/api/records/221072ae-2090-48a1-be6f-5a88f061431a.
73. J. Chave, Long term climatic water deficit; https://chave.ups-tlse.fr/pantropical_allometry.htm or https://chave.ups-tlse.fr/pantropical_allometry/CWD.tif.zip.
74. D. N. Karger, O. Conrad, J. Böhner, T. Kawohl, H. Kreft, R. W. Soria-Auza, N. E. Zimmermann, H. P. Linder, M. Kessler, Climatologies at high resolution for the earth's land surface areas. *Sci. Data* **4**, 170122 (2017).
75. T. Hengl, J. M. De Jesus, G. B. M. Heuvelink, M. Ruiperez, M. Kilibarda, A. Blagoti, W. Shangguan, M. N. Wright, X. Geng, B. Bauer-marschallinger, M. A. Guevara, R. Vargas, R. A. Macmillan, N. H. Batjes, J. G. B. Leenaars, E. Ribeiro, I. Wheeler, S. Mantel, B. Kempen,

SoilGrids250m: Global gridded soil information based on machine learning. *PLOS ONE* **12**, e0169748 (2017).

76. J. J. Danielson, D. B. Gesch, Global Multi-Resolution Terrain Elevation Data 2010 (GMTED2010) (U.S. Department of the Interior, U.S. Geological Survey, 2011).
77. O. Venter, E. W. Sanderson, A. Magrach, J. R. Allan, J. Beher, K. R. Jones, H. P. Possingham, W. F. Laurance, P. Wood, B. M. Fekete, M. A. Levy, J. E. M. Watson, Global terrestrial human footprint maps for 1993 and 2009. *Sci. Data* **3**, 160067 (2016).
78. C. M. Kennedy, J. R. Oakleaf, D. M. Theobald, S. Baruch-Mordo, J. Kiesecker, Managing the middle: A shift in conservation priorities based on the global human modification gradient. *Glob. Chang. Biol.* **25**, 811–826 (2019).
79. R. Crouzeilles, M. Curran, Which landscape size best predicts the influence of forest cover on restoration success? A global meta-analysis on the scale of effect. *J. Appl. Ecol.* **53**, 440–448 (2016).
80. M. Buchhorn, M. Lesiv, N.-E. Tsendbazar, M. Herold, L. Bertels, B. Smets, Copernicus Global Land Cover Layers—Collection 2. *Remote Sens.* **12**, 1044 (2020).
81. R. Genuer, J.-M. Poggi, C. Tuleau-Malot, Variable selection using random forests. *Pattern Recognit. Lett.* **31**, 2225–2236 (2010).
82. R. Genuer, J.-M. Poggi, C. Tuleau-Malot, VSURF R package (2019).
83. R Core Team, R: A language and environment for statistical computing (2021); www.r-project.org/.
84. N. J. Bloomfield, N. Knerr, F. Encinas-Viso, A comparison of network and clustering methods to detect biogeographical regions. *Ecography (Cop.)* **41**, 1–10 (2018).
85. FAO, "GLOBAL ECOLOGICAL ZONING FOR THE GLOBAL FOREST RESOURCES ASSESSMENT 2000" (Rome, 2001), (available at https://www.fao.org/3/ad652e/ad652e00.htm#TopOfPage).

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Strong floristic distinctiveness across Neotropical successional forests

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