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RESEARCH ARTICLE

Giants of the Amazon: How does environmental variation drive the diversity patterns of large trees?

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Abstract

For more than three decades, major efforts in sampling and analyzing tree diversity in South America have focused almost exclusively on trees with stems of at least 10 and 2.5 cm diameter, showing highest species diversity in the wetter western and northern Amazon forests. By contrast, little attention has been paid to patterns and drivers of diversity in the largest canopy and emergent trees, which is surprising given these have dominant ecological functions. Here, we use a machine learning approach to quantify the importance of environmental factors and apply it to generate spatial predictions of the species diversity of all trees (dbh ≥ 10 cm) and for very large trees (dbh ≥ 70 cm) using data from 243 forest plots (108,450 trees and 2832 species) distributed across different forest types and biogeographic regions of the Brazilian Amazon. The diversity of large trees and of all trees was significantly associated with three environmental factors, but in contrasting ways across regions and forest types. Environmental variables associated with disturbances, for example, the lightning flash rate and wind speed, as well as the fraction of photosynthetically active radiation, tend to govern the diversity of large trees. Upland rainforests in the Guiana Shield and Roraima regions had a high diversity of large trees. By contrast, variables associated with resources tend to govern tree diversity in general. Places such as the province of Imeri and the northern portion of the province of Madeira stand out for their high diversity of species in general. Climatic and topographic stability and functional adaptation mechanisms promote ideal conditions for species diversity. Finally, we mapped general patterns of tree species diversity in the Brazilian Amazon, which differ substantially depending on size class.

KEYWORDS
big trees, diversity map, forest ecology, forest inventory, remote sensing, species richness

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1 | INTRODUCTION

Understanding how the diversity of tree species is distributed is a great challenge, especially in tropical forests, a hyperdiverse biome. Once multiple plot inventories are combined, then they can reveal key large-scale patterning in community diversity, for instance, that some Amazon forests are extremely diverse (Gentry, 1988), or that wet Neotropical climates support high arboreal diversity (Clinebell et al., 1995). Multiple, recent initiatives that combine forest inventories have allowed further analysis of ecological and spatial variation over large scale (e.g., Bastin et al., 2018; Crowther et al., 2015; ForestPlots.net et al., 2021; Slik et al., 2015). These studies have confirmed that parts of South America and particularly western Amazonia, as well as the Andean foothills, are global epicenters for plant diversity and trees in particular (Cazzolla Gatti et al., 2022; Liang et al., 2022; Sabatini et al., 2022; Ter Steege et al., 2013).

More generally, it has long been known that the diversity of tree species follows latitudinal variations, consistent with the metabolic theory of biodiversity (Liang et al., 2022), or is affected by grain-dependent effects of both environment and biogeographic regions (Keil & Chase, 2019). In the Amazon basin tree diversity at the one-hectare scale are driven by gradients of precipitation and soil (Esquivel Muelbert et al., 2016; Ter Steege et al., 2003). However, most work focuses on trees with stems ≥10 cm in diameter, and sometimes as small as 2.5 cm diameter or less (Draper et al., 2021; Sabatini et al., 2022), meaning that diversity patterns among relatively small trees tend to dominate our understanding of tropical forest diversity. By contrast, few studies have attempted to analyze the largest trees at larger scales, let alone explore how environmental factors influence their diversity.

Large trees have a dominant influence on the aboveground biomass, productivity, and sustainable use of tropical forests (Ali et al., 2022; Fauset et al., 2015; Kearsley et al., 2019; Lindenmayer, 2017) and they are considered indicators of stable ecosystems (de Lima et al., 2022; Lindenmayer & Laurance, 2016; Roswell et al., 2021; Slik et al., 2013). However, even for the community of all tree species of all sizes, spatial diversity models are still scarce in Amazonia (Ter Steege et al., 2003, 2013), and primarily regional spatial diversity models for large trees are poorly studied. Thus, while we may expect divergent diversity patterns between small and large tree species, but have lacked the data or analyses to explore this in detail, and thus, key gaps remain concerning the main environmental factors driving diversity in the Amazon basin.

There are a few reasons to expect the diversity patterns of large trees to differ from those of smaller trees: (1) Areas of occupancy: Large trees can occupy larger areas than small trees, which means they can support more species in their habitat (Liu et al., 2019); (2) Habitat heterogeneity: Large trees can create different microhabitats in their structure, such as ecological niches at different tree heights, allowing different species to occupy specific areas (Mendieta-Leiva et al., 2022); (3) Habitat connectivity: Large trees can also serve as habitat connectors, linking different areas and allowing species to move between them. This can increase species diversity in an ecosystem (Craven et al., 2016; Keeley et al., 2021).

Positive relationships between plant diversity and environmental factors are common in various vegetation types (Balvanera & Aguirre, 2006; Beck et al., 2011; Slik et al., 2009; Zheng et al., 2019) and ecological gradients (Maharjan et al., 2021; Song et al., 2021; Tolmos et al., 2022; Venter et al., 2017; Wittmann et al., 2006). The available remote sensing environmental data provide spatially refined information on landscape and vegetation heterogeneity over the Amazon basin that can be readily incorporated into spatial models to study diversity distribution patterns. For example, the maximum large tree height in different biogeographic regions in the Amazon is influenced by edaphic, climatic, and topographic variables (Gorgens et al., 2021). These patterns might be expected to impact large tree diversity over space and/or time, depending on which factors are key—for example, the role of increased lightning occurrences and wind speed in limiting tree height suggests potential for concomitant changes in the diversity patterns of large trees (Bennett et al., 2015; Clark et al., 2019; Gora & Esquivel-Muelbert, 2021; Yanoviak et al., 2020).

The significant regional variation within the large Brazilian Amazon, and growing efforts to inventory tree plot biomass and species, favors the development of large area ecological and distribution models to understand how and which environmental factors influence the diversity of large and small trees. Here, using a multisite dataset from across the Amazon, we aim to explore how environmental factors influence patterns of total tree species diversity, and patterns of large trees, contributing to understanding how the forest is spatially structured and according to its biodiversity and environmental components.

2 | MATERIALS AND METHODS

2.1 | Study area

Individual tree data were obtained from 243 forest plots distributed across 65 sites in the Brazilian Amazon (Figure 1). Plot sizes and shape varied according to the objectives of each acquisition source. While the majority were standardized at 100 × 100 m (10,000 m^2), others are 40 × 250 m (10,000 m^2), 10 × 250 m (2500 m^2), 20 × 200 m (4000 m^2), and 20 × 50 m (1000 m^2). Only plots with at least 90% of the trees identified genus level and at least 60% to at species level, were included in the analysis. Thus, we included 108,450 trees with a stem diameter of 1.30 m from the ground (dbh—diameter at breast height) ≥ 10 cm in the analyses.

A subset of the data was created by filtering only trees with dbh ≥ 70 cm, highlighting the largest trees, as suggested by Harris et al. (2021). The choice of large trees with a diameter ≥70 cm can be consulted for more details in Appendix S3. This subset had 240 plots and 3863 trees. All plots contribute to the wider ForestPlots.net meta–network and database (https://www.forestplots.net/), which curates inventories conducted over the last 25 years (1997–2021) (ForestPlots.net et al., 2021). Our sites span different forest types and cover several biogeographic regions. To ensure the comparison of plots with different sample sizes, plot data were

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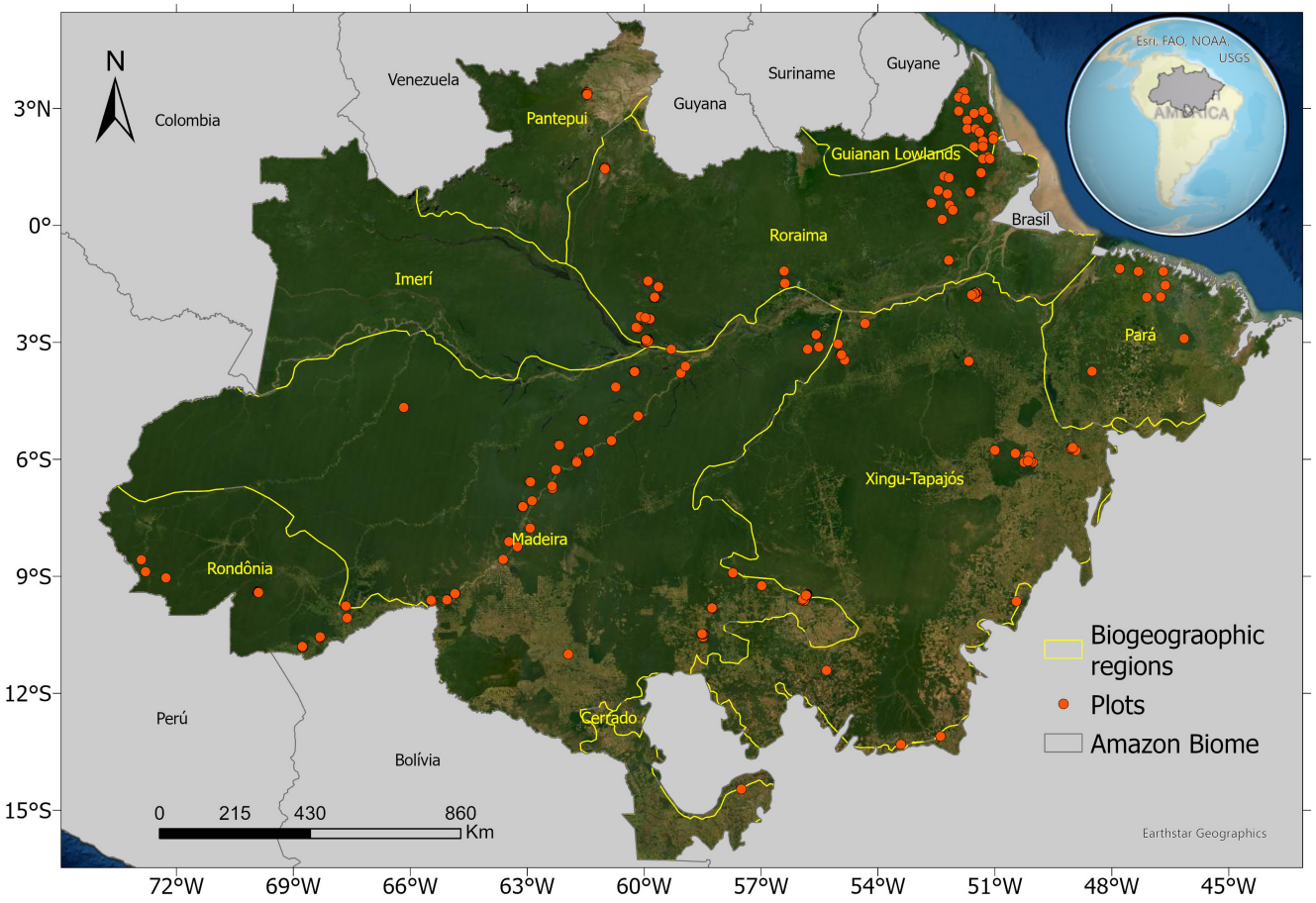


FIGURE 1 Distribution of plots in the Brazilian Amazon and delimitation of the biogeographic regions in the biome scale. [Colour figure can be viewed at wileyonlinelibrary.com]

standardized to the 1 ha sampling effort (Bastin et al., 2018; Clark & Clark, 2000).

Taxonomic nomenclature was checked using the Taxonomic Name Resolution Service (https://tnrs.iplantcollaborative.org) and Missouri Botanical Garden (https://www.missouribotanicalgarden.org/). To verify any uncertainty in the correct name of the species, we used the taxonomic conference implemented in the flora package (Carvalho, 2020) for R software version 4.2.1 (R Core Team, 2022).

2.2 | Species diversity

Diversity was analyzed for all trees (dbh ≥ 10 cm) and for large trees only (dbh ≥ 70 cm), using the Fisher's alpha-diversity index (α) and Shannon entropy diversity index calculated for each plot:

$$S = \alpha \ln\left(1 + \frac{n}{\alpha}\right) \quad (1)$$

$$e^{H'} = \exp\left(-\sum_{i=1}^{S} (P_i) \times \ln(P_i)\right) \quad (2)$$

Tree alpha diversity, expressed as Fisher's alpha (α), is a measure which corrects for the sample size (Fisher et al., 1943). The exponential Shannon entropy index is a transformation of Shannon's index that weights species in proportion to their frequency (Jost, 2006); n is the number of individuals. H' is the Shannon diversity index; S is the total number of species for a given plot; P_i is the proportion of the total number of individuals in the sample belonging to species i. The Shannon index provides information on abundance and equability without favoring any species, as it counts all species according to their frequencies (Borges Silva et al., 2022). To complement the information on the diversity index, the richness resulting from the total number of species was also calculated for each plot. Richness and diversity are considered indicators of general biodiversity (Gastauer et al., 2021). All data were analyzed using the *vegan* (Oksanen et al., 2022) and *BiodiversityR* packages (Kindt, 2022) in R.

Rarefaction curves of cumulative individuals were created, one for each dataset, using the *iNEXT* package (Hsieh et al., 2022).

2.3 | Environmental variables

Sixteen candidate spatially explicit environmental variables were selected and grouped into three distinct categories: topographic, climatic, and edaphic (Table 1). To allow comparison of our results with those from other studies, we used the same variables as considered in the work developed by Gorgens et al. (2021). Data were cropped considering the limits of the Brazilian Amazon and re-sampled to a spatial resolution of 30 arc seconds (~1 km) when necessary.

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TABLE 1 List of the main environmental variables selected for this study.

Environmental variable					
Category	**Subcategory**	**Name and unit**	**Abbreviation**	**Spatial resolution (period)**	**Source**
Topographic	Elevation	Elevation above sea level (m)	elev	30 m	SRTM
Climatic	Temperature	Mean annual temperature (°C)	tannual	30 arc seconds	WorldClim
		Maximum temperature (°C)	tmax	30 arc seconds	WorldClim
		Temperature seasonality (%)	tseason	30 arc seconds	WorldClim
	Precipitation	Average annual precipitation (mm)	pannual	30 arc seconds	WorldClim
		Precipitation seasonality (%)	pseason	30 arc seconds	WorldClim
		Precipitation of the wettest month	pwettest	30 arc seconds	WorldClim
	Other climatic	Number of clear days per year (days)	clearDays	500 m (2014–2018)	MODIS
		Days with precipitation greater than 20 mm (days)	days20	0.05 degrees (2014–2018)	CHIRPS
		Potential evapotranspiration (mm $year^{-1}$)	pet	2.5 arc minutes (1990–2016)	TerraClimate
		Fraction of absorbed photosynthetically active radiation (%)	fapar	0.05 degrees (2016–2018)	NOAA AVHRR
		Lightning rate (flashes rate $year^{-1}$)	lightning	0.1 degrees	LIS TRMM
		Meridional speed (N–S) (m s^{-1})	vspeed	0.25 degrees (2014–2018)	ECM-RWF
		Zonal speed (W–E) (m s^{-1})	uspeed	0.25 degrees (2014–2018)	ECM-RWF
Edaphic	Fraction of clay content	Soil structure physical properties water availability (%)	clayContent	250 m	SoilGrids
	Fraction of water content	Soil structure physical properties water availability (%)	waterContent	250 m	SoilGrids

Note: Variable categories, subcategories, names, and their corresponding units and abbreviations are shown.

Temperature, precipitation, and the 19 bioclimatic variables were downloaded from WorldClim version 2 (Fick & Hijmans, 2017). The average number of cloudless days throughout the year was obtained from the surface reflectance products of the MODIS (Moderate Resolution Imaging Spectroradiometer) sensor. The Terra product MOD09GA Version 6 was used, which provides an estimate of the spectral reflectance of the MODIS surface, corrected for atmospheric conditions.

The average number of days per year with precipitation above 20 mm has been calculated from the precipitation time series of the Climate Hazards Group InfraRed Precipitation with Station (CHIRPS) dataset (Funk et al., 2015). Potential evapotranspiration was obtained from TerraClimate data, which combine climatological normals from WorldClim, the Climate Research Unit (CRU) Ts4.0, 55-year Japanese Reanalysis (JRA-55) data, and the Penman–Monteith methodology. Fraction of absorbed photosynthetically active radiation (fapar) was obtained from the calibrated and corrected Earth surface reflectance product of the Advanced Very High-Resolution Radiometer (AVHRR) of the National Oceanic and Atmospheric Administration (NOAA). The fapar layer provides information on the photosynthetic activity of plants (Baret et al., 2013).

Lightning frequency is associated with climatic events and tree mortality (Gora et al., 2020). This variable was obtained from the Lightning Imaging Sensor (LIS) instrument aboard the Tropical Rainfall Measuring Mission provided by the Global Hydrology Resource Center of NASA's Earth Observation System (EOSDIS).

Wind speed data were made available from the maximum daily average wind speeds over the last 5 years produced by the fifth reanalysis of the global model (ERA5) of the European Center for Medium-Term Weather Forecasts (ECMWF). Two metrics of wind speeds were used: u-speed, which is the zonal speed (a component of the wind toward the east), and v-speed, which is the meridional speed (a component of the wind toward the north). Studies indicate that winds are related to disturbances that result in tree mortality in the Amazon (Marra et al., 2014; Rifai et al., 2016).

Edaphic variables were obtained from the SoilGrids based on the World Reference Base (WRB) and USDA classification systems (ca. 280 raster layers in total; Hengl et al., 2017). The layers of clay content (% fine particles <2 μm) and water content (% volumetric at field capacity at 30 cm), both with a spatial resolution of 250 m, were estimated from machine learning applied over a global profile

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compilation and soil layers (Hengl et al., 2017). All variables were processed using ArcMap 10.1 (ESRI, 2019), and analysis was performed using R software version 4.2.1 (R Core Team, 2022).

2.4 | Spatial modelling

Choosing the suitable algorithm for modelling depends on the problem and avaiable data. Here we used the Random Forest algorithm to model the relationship between environmental variables and diversity using 500 random, regression–type decision trees. According to the approach carried out by Meyer and Pebesma (2022), the Random Forest (RF) algorithm is widely used for data analysis of plant diversity, mainly to understand patterns, due to several reasons: (1) effectively handles high-dimensional data: rainforests contain a wide variety of species, which results in highly complex, high-dimensional data. RF can handle this complex data and produce accurate results; (2) it is a nonparametric algorithm: as the relationships between species in a rainforest can be highly nonlinear, a nonparametric algorithm such as RF is best suited to handle these data types; (3) Can handle missing data: according to Cai et al. (2023), data collected in tropical forests may need to be completed or have missing values. RF can handle this missing data without dropping or replacing it; (4) can handle overfitting: the presence of rare species in a tropical forest can lead to an overfitting problem, where the model is overfitted to the available data and RF is less prone to this problem due to its ensemble model nature, where many smaller models are combined to produce an overall result; (5) it is highly scalable: The RF algorithm is highly scalable and can be easily applied to larger datasets, which is an advantage in a rainforest environment where the number of species can be large.

For all these reasons, RF is widely used for data analysis in tropical forests to understand diversity patterns. However, this does not mean that other machine-learning algorithms cannot be used to analyze rainforest data or other data types. Choosing the suitable algorithm depends on the problem and available data.

The number of variables randomly sampled as candidates in each division was defined as the number of explanatory variables divided by 3 (default algorithm parameterization). Evaluation of the model's accuracy was performed using the standard error of the estimate (RMSE) and coefficient of determination (R^2), considering the *k*-fold cross-validation ($k=15$). The importance of environmental variables was analyzed using marginal graphs, keeping the other variables constant at an average value. The importance of variables is measured by permuting variables in the model and measuring the increase in estimation error (MSE).

The RF model was applied to the environmental layers at the pixel level, for the entire Amazon region, through map algebra. The model parameters were applied independently to each pixel to produce the diversity maps for all trees and for the giant trees of the Amazon forest (Figure 2). Statistical analysis was applied in an R environment (R Core Team, 2022), using the MASS (Ripley et al., 2022) and RandomForest (Cutler & Wiener, 2022) packages.

3 | RESULTS

3.1 | Species diversity

Considering only the large trees (dbh ≥ 70 cm), 240 plots had 3863 individuals (~3.6% of the measured trees) grouped into 449 species (for every 8.6 trees, one large species was found). The lack of a plateau indicates that many additional species are likely to be discovered if sampling increases (Figure 3a). Considering all trees measured (dbh ≥ 10 cm), the rarefaction curve reached a plateau with approximately 25,000 individuals distributed in approximately 240 species in a total of 2832 species sampled (Figure 3a). Fisher's alpha diversity of all trees showed a poor, but significant correlation ($r=.2$, $p<.001$) with the Fisher's alpha diversity of large trees (Figure 3b). The median Fisher's alpha-diversity index for all trees (101) was approximately 94% higher that for large trees (4).

3.2 | Spatial modelling and environmental factors

The fitted RF model showed a standard error of 0.69 (MAE = 3.22; RMSE = 4.81) for large trees and 0.65 (MAE = 29.14; RMSE = 41.7) for all trees. The variation explained by the RF models was markedly high for Fisher's alpha diversity all trees ($R^2=.71$) and for Fisher's alpha diversity large trees ($R^2=.85$). The graphical analysis of observed versus predicted diversity data shows positive associations, with a higher degree of adherence for all trees compared to large trees (Figure 4).

The 16 environmental variables considered in this study showed different degrees of importance when analyzing the association between large trees and trees in general (Figure S1). Four different degrees of association were observed: positive (diversity increases as the factor increases), negative (diversity decreases as the factor increases), paraboloid behavior with downward concavity (diversity initially increases but then decreases as the factor increases), and upward concave paraboloid behavior (diversity initially decreases but increases as the factor increases). Furthermore, these environmental variables can be divided into two groups: environmental variables associated with tree growth resources and those with disturbances. Although some variables can reflect both resources and disturbances, to facilitate the discussion, we here associate variables of this type with the most relevant of the two categories. The environmental variables associated with disturbances (uspeed, vspeed, lighting, days 20) were the most relevant for the diversity of large trees. The variables associated with tree growth (clearDays, pseason, pwettest, elevation, pannual, pet, tannual, and fapar) were the most relevant for the diversity of trees in general (Figures 5 and 6).

Among the variables associated with disturbance, wind speed, lightning occurrence rate, the number of days with precipitation above 20 mm, and the maximum temperature stand out. These variables are generally directly related to tree mortality and were more relevant to the diversity of large trees than to the diversity of all trees (Figure 5b–e). While four of these variables above are among the six most relevant for the diversity of giant trees, only three are

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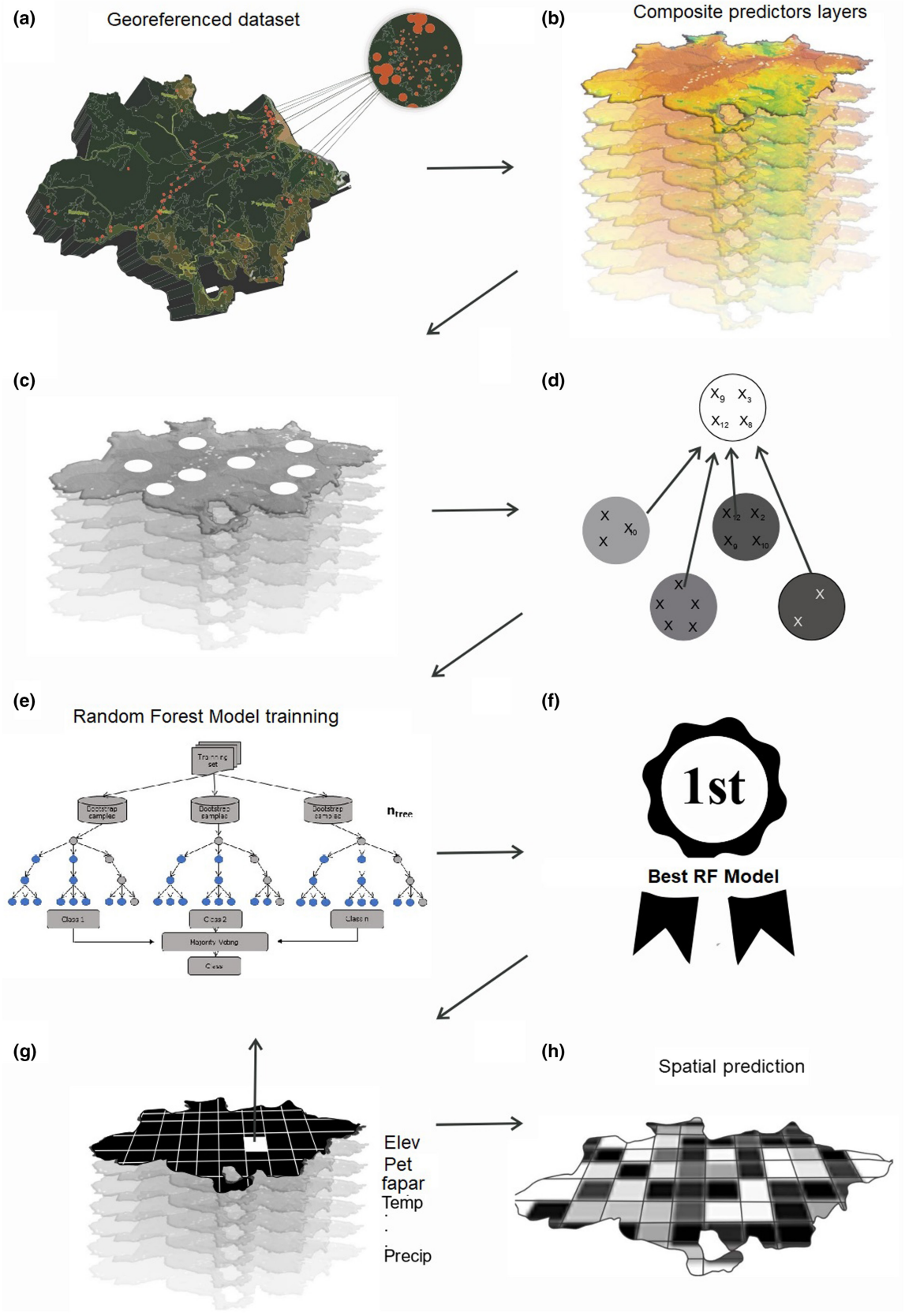


FIGURE 2 Data processing and analysis flowchart: (a) plot network organization; (b) stacking of environmental spatial layers; (c) crossing the field plots and the stack of environmental variables; (d) for each forest typology and biogeographic region, we submitted plot records to identify the least collinear collection of covariates; (e) fitted of the Random Forest model for diversity; (f) a top-tier predictive model was selected or created by averaging the model using cross-validation; (g) diversity estimation for the entire Amazon at the pixel level; and (h) distribution of diversity for all trees and for large trees. [Colour figure can be viewed at wileyonlinelibrary.com]

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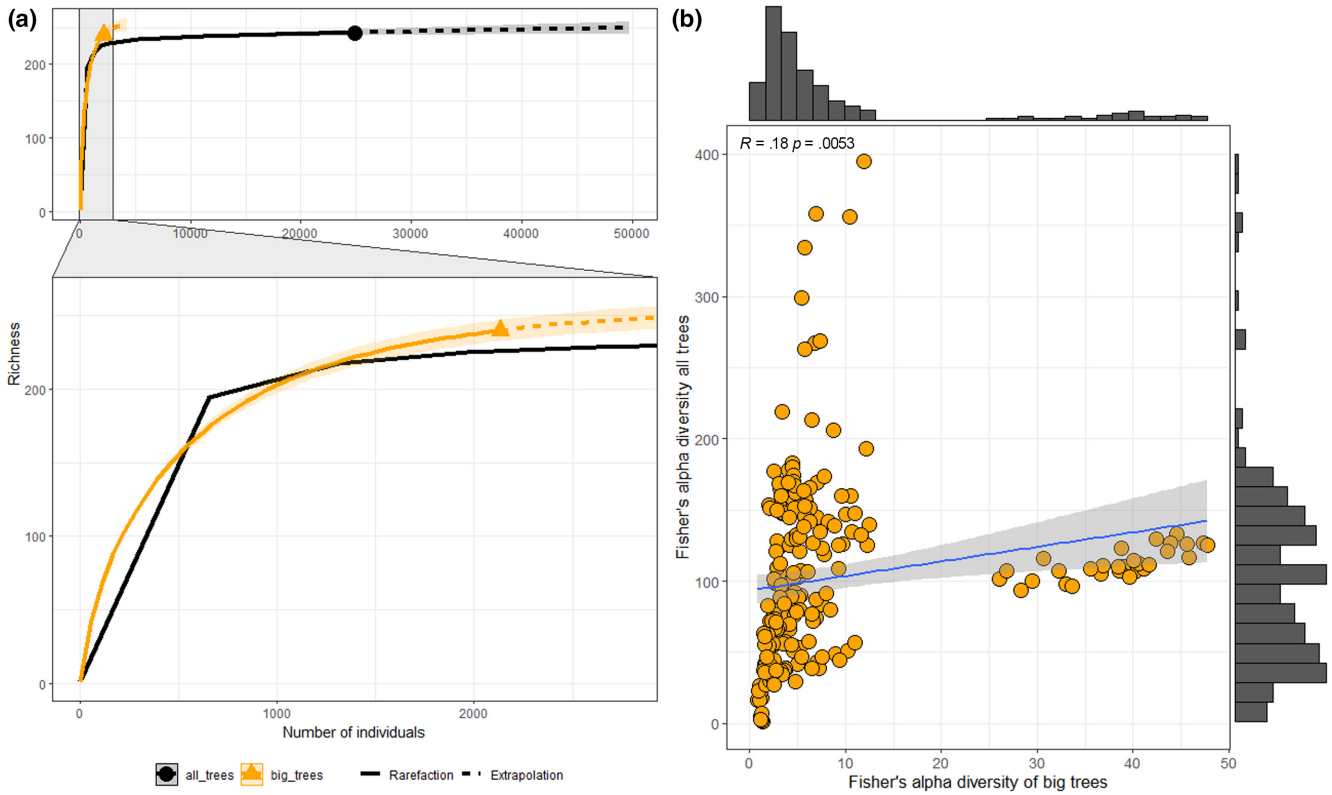


FIGURE 3 Comparison of rarefaction curves based on sample size (solid lines) and extrapolation (dashed curves) of species diversity of large trees and set of all trees (a). It is expected that greater species richness of large trees will be identified for the same number of individuals sampled, compared with the group of all trees already approaching a plateau. The bootstrap method obtained the 95% confidence intervals (shaded regions) based on 1000 repetitions using the iNEXT package algorithm (Hsieh et al., 2016). The reference samples of individuals are zoomed in to highlight the slight difference in species richness for the two datasets analyzed. (b) Relationship between Fisher's alpha-diversity metrics for large trees and the set of all trees measured in different locations in the Amazon biome. The solid line refers to a trend with statistical significance (.05), and the area around the line sets up a 95% confidence interval. Marginal histograms indicate the frequency and distribution of values. There is a low frequency and decrease in the values of the diversity metrics for both cases. However, this modest but significant correlation suggests that a single tree of just one species can significantly increase diversity at the plot level (de Lima et al., 2022). [Colour figure can be viewed at wileyonlinelibrary.com]

among the six most relevant considering all trees. Climatic metrics derived from precipitation (pannual and pseason) are of greater predictive importance for diversity indices analyzed and RF models.

Among the environmental variables associated with resources are photosynthetically active radiation, precipitation metrics (annual average, wettest month, and coefficient of variation), temperature metrics (annual average and coefficient of variation), number of days without clouds, evapotranspiration, elevation above sea level. These variables were the most strongly associated with all tree diversity (Figure 6a, c, e–g, l–n).

Average annual precipitation, the number of annual days with precipitation greater than 20 mm, evapotranspiration, precipitation of the wettest month, elevation, and soil clay content were positively associated with the Fisher's alpha diversity of big trees. However, the factors lightning occurrence rate, component meridional wind speed, zonal wind speed, precipitation variation coefficient (pseason), mean annual temperature, number of annual days without cloud, and maximum annual temperature showed a negative association. The factors photosynthetically active radiation, coefficient of temperature variation, and soil water content showed a paraboloid association with Fisher's alpha diversity, with upward concavity (Figure 5).

The Fisher's alpha diversity of large trees increased substantially with average annual precipitation, elevation, and a fraction of photosynthetically active radiation with a threshold above 80% and number of days with precipitation greater than 40 mm. In contrast, increased wind speed and lightning occurrence rate are associated with lower Fisher's alpha diversity of large trees (Figure 5).

Considering the Fisher's alpha diversity of all trees, the number of annual days with precipitation greater than 20 mm, lightning occurrence rate, average annual precipitation, elevation, and photosynthetically active radiation, and average annual temperature showed a positive association with diversity. In contrast, the factors coefficient of variation of precipitation, number of annual days without cloud, evapotranspiration, and soil water content showed a negative association. Precipitation of the wettest month, zonal wind speed, meridional wind speed, maximum temperature annual, coefficient of temperature variation, and soil clay content showed a paraboloid association with upward concavity with the total tree diversity (Figure 6).

The highest Fisher's alpha-diversity values for large trees were higher in terra-firme forest in the northern portion of the Guiana Shield biogeographic province and the eastern portion of the Roraima biogeographic province (about −54 to −51° longitude, Figure 7). Fisher's alpha

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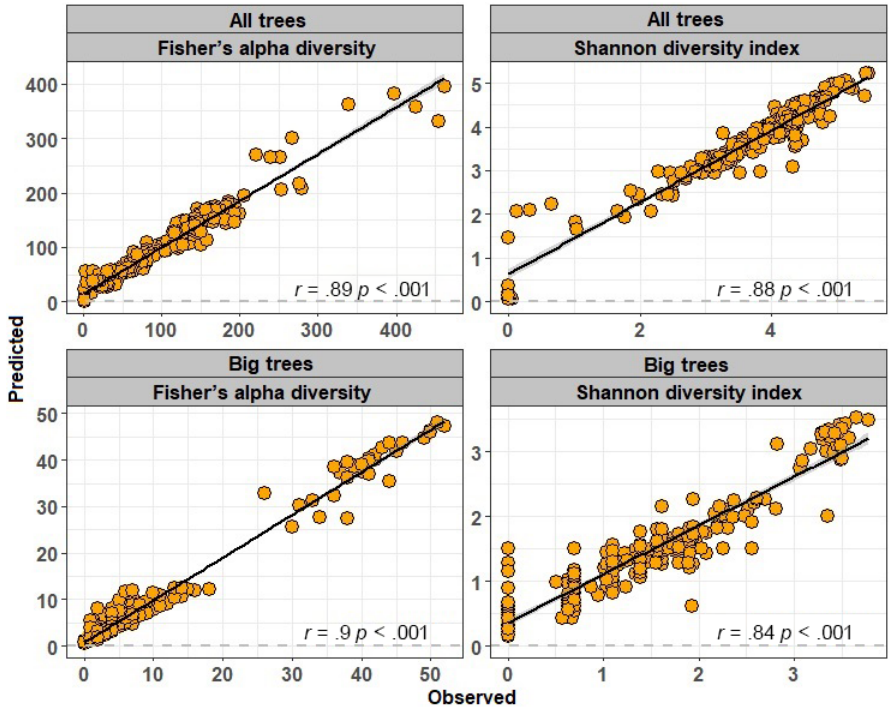


FIGURE 4 Correlations between observed and predicted diversity values by the Random Forest model for the 243 plots. The straight line indicates the predicted best fit for each case. [Colour figure can be viewed at wileyonlinelibrary.com]

of large trees in this region exceeded 40. The predictive maps also reveal many areas with intermediate alpha-diversity values for large trees (10 < 20) in areas west of Imerí, Madeira, and north of Xingu-Tapajós and Pantepui. Large areas in central Amazonia between Xingu-Tapajós and Madeira and its tributaries are dominated by forests with low alpha diversity of large trees (<6). The central and eastern provinces (Madeira, Xingu-Tapajós, and Pará) are dominated by open ombrophilous forests (also known as rainforest or tropical rainforest, is a type of ecosystem that develops in tropical and subtropical regions with high rainfall throughout the year). The areas of ecological tension or transition belt showed the lowest diversity values for all trees and large trees (Figure 7). These regions coincide with the arc of deforestation.

The relationships between environmental factors and the Shannon diversity index produced trends similar to those based on the Fisher's alpha for both large (Figure S4) and all trees (Figure S5). However, a spatial appreciation for this index suggests a significant divergence in the potential distribution of the diversity of large species and the set of all analyzed species (Figure S6). The greatest Shannon diversity for all trees was observed in the Imerí province, northwest of the Madeira and Pantepui regions, closely associated with forests with high rainfall. The supplementary information results can reveal more details of the correlation analysis for the estimated diversity metrics versus the inventoried plot size (Figure S2) and the number of large trees (Figure S3).

4 | DISCUSSION

4.1 | Species diversity and environmental factors

In this study, we asked what factors explain the diversity of large trees (dbh ≥ 70 cm) in the Amazon and how these patterns differ from those affecting smaller trees (dbh ≥ 10 cm). We show that the diversity of large trees is mainly determined by environmental factors linked to the intensity of disturbances. In contrast, the diversity of smaller trees is more affected by factors that control productivity. Higher diversity values for large trees were found in the extreme Northest of Amazonia (Amapá), while the highest values for smaller trees were found in the Northwest.

We found that the diversity of large trees decreased with increasing meridional wind speed and lightning occurrence rate. Large trees that emerge above the forest canopy are most susceptible to lightning strikes and toppling by wind due to the greater exposure to these factors (Bennett et al., 2015; Clark et al., 2019; Gora & Esquivel-Muelbert, 2021; Yanoviak et al., 2020). Recent research shows that lightning has been a prominent cause of crown damage in the tropics, often leading to tree mortality (Gora et al., 2017, 2021; Marra et al., 2014).

The highest diversity of large trees was found in terra-firme areas (well-drained rainforest including on hills) in the Guiana Shield and Roraima regions. These regions also have the greatest potential for the growth of very tall trees (Gorgens et al., 2021). This strong relationship between well-drained upland areas and large tree diversity has also been observed in other forests in the tropics and has been associated with ecologically stable environmental conditions for tree establishment and growth (Duivenvoorden, 1995; Fagua et al., 2021; Slik et al., 2009; Ter Steege et al., 2003; Venter et al., 2017).

Recurrent increases in wind speed can significantly modify the structure and composition of forests. For example, the predicted change in tropical cyclone regimes due to climate change can strongly impact forests in the tropics (Hall et al., 2020; Rau et al., 2022; Rifai et al., 2016). Our largely equatorial forests are not affected by cyclones but strong winds associated with convectional storm downbursts, and also cold fronts in southern and western Amazonia, may drive significant mortality for large trees. Since most trees in the forest are not

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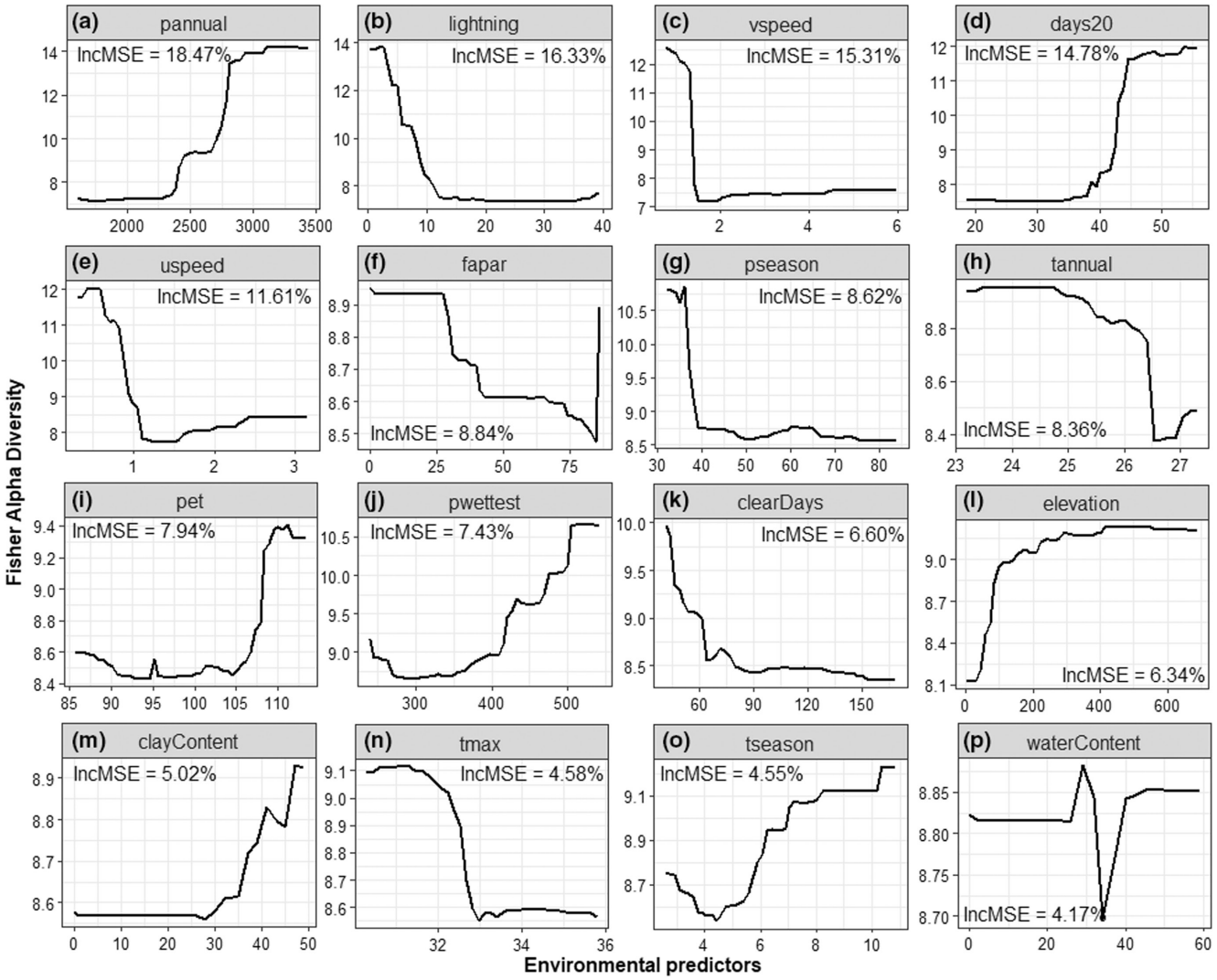


FIGURE 5 Graphs of the marginal effect of each environmental variable on the diversity of large trees (dbh ≥ 70 cm) in the Random Forest model. The environmental factors are shown in order of decreasing importance.

large (dbh ≥ 70 cm), lightning and wind are much less important for the set of all trees (dbh ≥ 10 cm). Furthermore, wind and lightning are essential factors in the diversity and dynamics of species since they are considered to be agents of natural disturbance in forests and can act by selecting individuals (Hall et al., 2020; Kling & Ackerly, 2021; Laurance & Curran, 2008; Mitchell, 2013; White & Pickett, 1985).

Our results show higher diversity for trees in general (dbh ≥ 10 cm) in low-altitude forest regions with permanent, seasonal, or transitional (ecotone) flooding along the Imeri province (Figure 7). This region is dominated by extensive river systems, floodplains, and lowlands. Depending on their proximity to rivers and their sediment load and topography, forests contain great diversity. These results are possibly expected because these areas are among the lowest densities of human population in the Amazon region, and roads are absent, giving them a particular value in conservation. Areas that are low or humid have trees with smaller crowns (Barbier et al., 2010) but with high species heterogeneity, mainly because they are ecotones or forest transition areas (Amaral et al., 2021; Marques et al., 2011; Silveira et al., 2016). These wetlands are also hotspots for endemic flora and fauna (Berde et al., 2020; Morrone, 2014) and contribute significantly to regional and global biodiversity (Junk et al., 2006; Liang et al., 2022). Similar results have been found in floodplain areas at the Biome scale (Duivenvoorden, 1995; Moraes et al., 2021; Silman et al., 2007; Ter Steege et al., 2013; Wittmann et al., 2006). These diversity patterns are also observed in the context of source–sink effects along topographic gradients (Colville et al., 2020; Maharjan et al., 2021; Nanda et al., 2021; Syfert et al., 2018; Zelený et al., 2010) and along latitudinal gradients (Kraft et al., 2011; Roy et al., 2007; Slik et al., 2009). This would mean that on evolutionary timescales, these ecological mechanisms of lowland forests are essential for maintaining tree diversity in tropical mountain forest (Coelho de Souza et al., 2019; Slik et al., 2009).

The three variables related to precipitation were among the most important associated with the diversity of all trees (dbh ≥ 10 cm).

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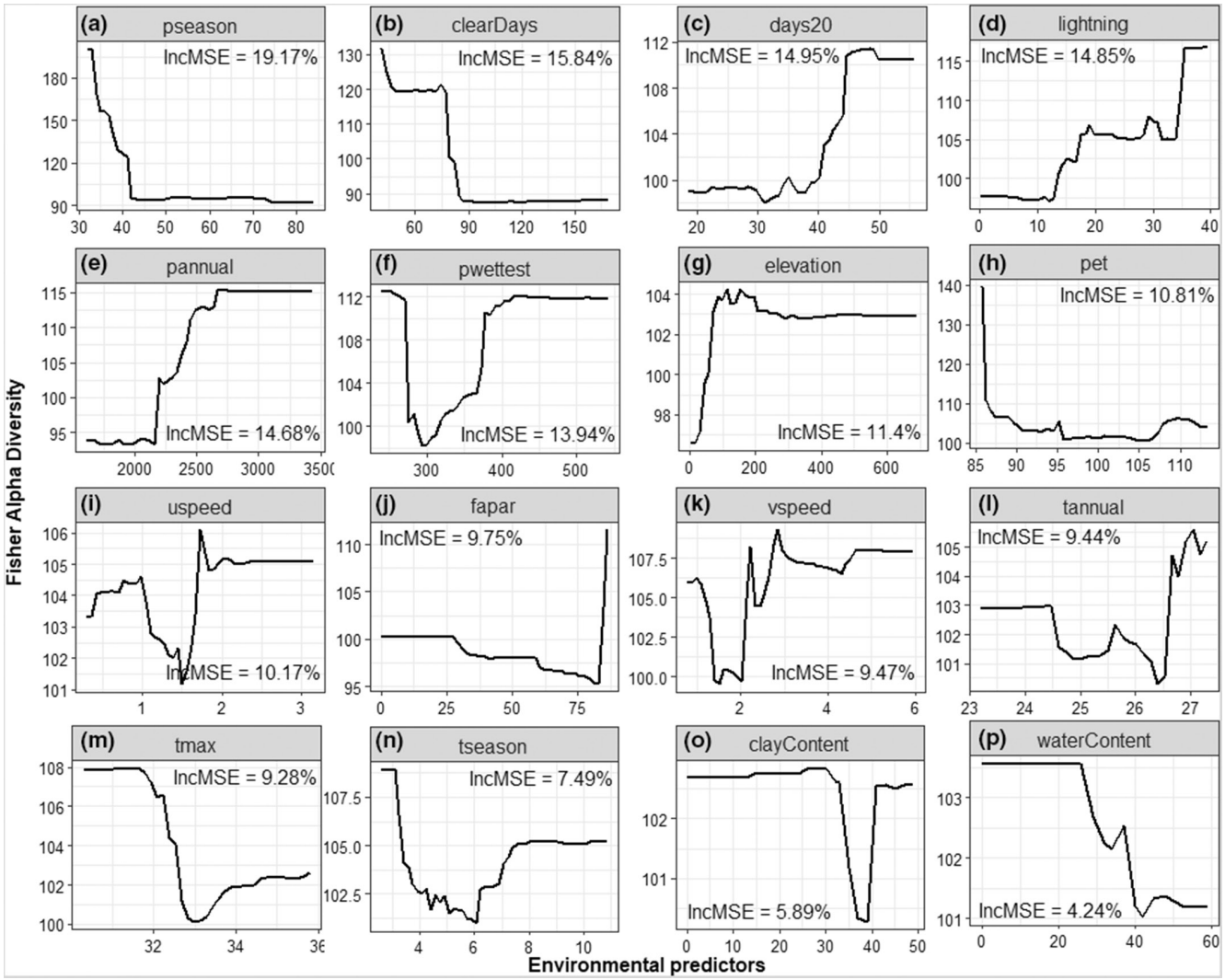


FIGURE 6 Graphs of the marginal effect of each environmental variable on the diversity of all trees (dbh ≥ 10 cm) in the Random Forest model. The environmental factors are shown in order of decreasing importance.

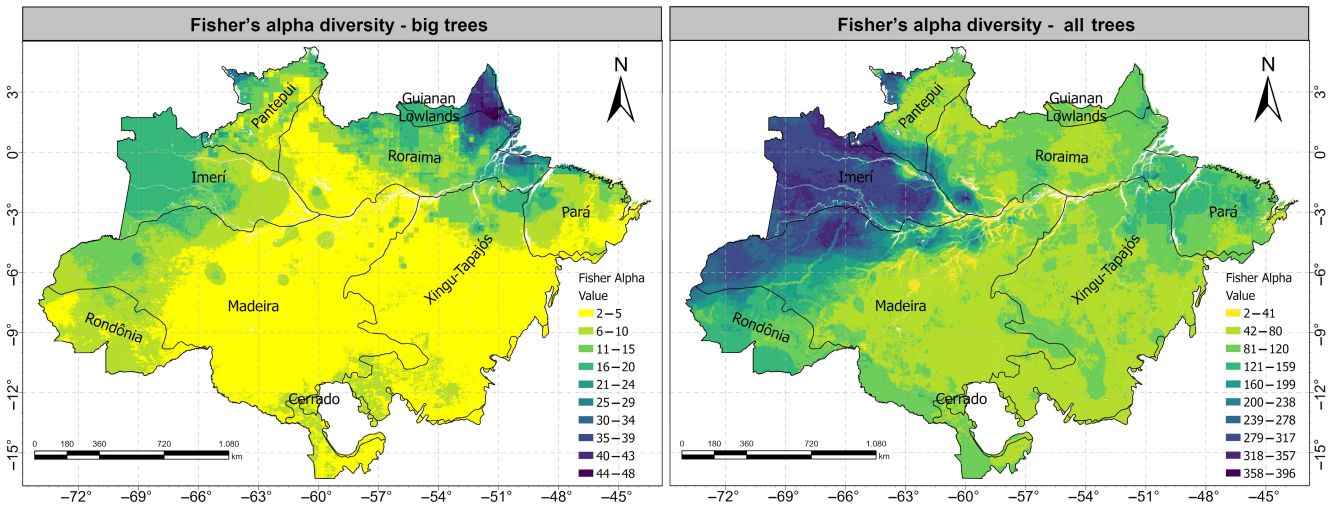


FIGURE 7 Fisher's alpha-diversity distribution for large trees (dbh ≥ 70 cm) and diversity distribution considering all trees (dbh ≥ 10 cm) estimated by the RF model for the Brazilian Amazon. [Colour figure can be viewed at wileyonlinelibrary.com]

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Rainfall in Amazonia averages approximately 2300 mm year^{-1}, and is driven in part by the austral monsoons and generates a well-defined environmental gradient. In areas near the Brazilian borders with Colombia and Venezuela, the annual total rainfall can reach 3500 mm (Figueroa & Nobre, 1990). Here, there is no defined dry period, with potential to flood some forests most of the year (Householder et al., 2021; Junk et al., 2018). These high precipitation values are associated with less seasonal equatorial climates, and near the Andes mountains, rainfall is further enhanced by the orographic rise of moisture transported by the east trade winds of the Intertropical Convergence Zone (ITCZ).

Various studies report changes in tree species composition along tropical altitudinal gradients (Guimaraes et al., 2021; Tolmos et al., 2022; Venter et al., 2017). In our analyses, lower rainfall and lower elevation (<50 m a.s.l.) in certain areas are associated with decreases in the diversity indices both for large trees and for the set with all trees (Figures 5–7). In these environments, the lower areas are characterized by communities of taxa that have difficulty growing to reach large dimensions (Da Cunha et al., 2021).

The annual number of days without clouds (clearDays year^{-1}) and the seasonality of precipitation (pseason %) were essential predictors to explain the patterns of diversity of all trees (Figure 6). However, they were of only intermediate importance for the diversity of large trees (Figure 5). An increase in cloudless days is associated with direct solar radiation (Barkhordarian et al., 2019; Gorgens et al., 2021), favoring photosynthetic activity for the species pool up to a thermal tolerance threshold (Green et al., 2020; Sullivan et al., 2020). Although atmospheric dryness, caused by the combination of these factors, can increase photosynthetic activity in the Amazon forest when water supply is abundant (Green et al., 2020), reductions in diversity in southern Amazonia may result from the long exposure of plants to high solar radiation and associated extended periods of seasonal water deficit. Bennett et al. (2015) found that droughts consistently negatively impacted larger trees' growth and mortality rates on a global scale. Other studies report that the number of clear days and the seasonality of precipitation are determinant factors for floristic diversity patterns at regional and continental scales (Bruijnzeel et al., 2011; Ehbrecht et al., 2021; Jiang et al., 2017; Wagner et al., 2016; Wilson & Jetz, 2016).

Elevation, here treated as a proxy for distinguishing terra-firme from floodplains, had a significant positive association with the diversity of both trees in general and large trees. Studies in tropical forests of Borneo (Slik et al., 2009), tropical lowlands of South America (Neves et al., 2020), Tanzania (Tallents et al., 2005), Colombia (Fagua et al., 2021; Tolmos et al., 2022), and Papua New Guinea (Venter et al., 2017) have also reported the importance of altitude in species diversity and composition.

4.2 | Study limitations

In the meta-analysis performed, we explored a variety of data sources and analytical tools that can be applied to develop predictive maps that incorporate the observed spatial pattern of diversity in biome-scale landscapes, forest types, and biogeographic regions. However, available data still lacks good coverage or resolution for some areas, leading to potential limitations.

First, it is common to face problems using inventory data collected differently in each location, mainly associated with taxonomically reliable data, and correctly defined forest typologies in a given locality. As a result, some species common in the biome may go unnoticed, and not all forest types may be equally represented, leading to high standard deviations or biased diversity estimates for each forest type or biogeographic region (Slik et al., 2009). Although the locations were spatially well distributed for the biome, some locations were close to one another. An effort was also made to correct taxonomic names in specialized websites and packages and in using maps of forest typologies in finer detail. This procedure was necessary to correct errors about the representativeness of forest typologies and species richness at the plot level and the biome scale (Ter Steege et al., 2016). The analysis of the diversity patterns discussed is also based on accurate classifications of land cover and markedly anthropic gradients, which may not be available or may occasionally be misaligned with the inventoried plots (Schmit et al., 2006).

Second, different scales of environmental data (10 × 10 km tables) and inventory form another complication, as plots covering a few hectares are unlikely to represent a 10 × 10 km area (Slik et al., 2009). In addition, some regions or areas contained more inventoried trees, plots, or surveyed surface area than others, resulting in different levels of diversity captured by the site. Although attempts have been made to correct the diversity values for these sampling biases, likely, they have at least partially influenced the results. Ideally, meta-analyses such as this should be performed on standardized plot layouts in combination with high-resolution environmental data (e.g., Gerstner et al., 2017). Unfortunately, such an approach is still difficult to carry out in more remote tropical areas in the Amazon, where the availability of reliable inventory data is already a problem (ForestPlots.net et al., 2021), not to mention reliable high-resolution soil and climate data (Fick & Hijmans, 2017).

Third, and related to environmental layers and their potential to explain the diversity of large trees, it was noted that the functional importance of edaphic variables (clayContent and waterContent) presented the poorest results among all the variables tested based on related characteristics to predictive importance. These low-importance values obtained can be explained perhaps by the available GIS layers in which the spatially explicit grid (interpolated values) does not correctly explain the inherent values at the plot level, thus requiring an effort to collect data at local scales. A detailed investigation of these factors locally would be fundamental, as it could identify other ecological functions of the edaphic information set for the diversity of tree species in the Amazon (Marca-Zevallos et al., 2022; Terra et al., 2018). Edaphic factors are fundamental in explaining many attributes and ecological patterns of the forest, mainly related to productivity and diversity in tropical forests (Hofhansl et al., 2020; Homeier & Leuschner, 2021). Joswig et al. (2022) find a dominant joint effect

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of climate and soil on trait variation of plant functional characteristics on a global scale. However, our results are consistent with studies of the same tropical geographic regions (e.g., Ter Steege et al., 2013) with highly varied species composition (Slik et al., 2015), which leads us to believe that the main conclusion is satisfactory. Finally, more direct studies on the set of ecological forces acting to define patterns of tree species diversity are needed to clarify these responses.

4.3 | Final considerations

We conclude that the patterns and processes that determine the diversity of large trees clearly differ from those for smaller trees, which has clear implications for ecological theories, conservation, and management.

Although the RF models suggest that the diversity of large trees (dbh ≥ 70 cm) and of all trees (dbh ≥ 10 cm) is associated with different environmental variables, there is a modest and significant association ($r = .2$, $p < .001$) between the two Fisher's alpha-diversity indices (Figure 3b).

Richness is strongly associated with the number of individuals in the sample, especially in the early stages of sampling (Figure 3a). Furthermore, as the sampling proceeds, the rarefaction curves representing communities with trees of different sizes intersect twice, first in a number slightly more significant than 5000 individuals and then in a number slightly <1500 individuals. This means that the relative richness of two datasets (albeit in the same samples), measured on smaller numbers of individuals, does not predict well their relative richness on a larger sample size. This is generally true even when using Chao1 estimators (Chao et al., 2004; Roswell et al., 2021) to predict true diversity. Because richness is so sensitive to sampling effort and relative abundance, its estimate may depend on how samples are patterned. Even the best estimators of asymptotic richness, such as Chao1 (Colwell et al., 2012), cannot reliably predict true community diversity (Jost, 2007). The problem is that both the sample richness and the individual-based richness estimators are strongly influenced by the rarest species, which are precisely the species about which we know less and which are more challenging to identify in the field. This is another way of saying wealth has high uncertainty (Roswell et al., 2021). Indeed, this uncertainty is often insurmountable in estimating and comparing community diversity from samples.

The resulting maps are a potential distribution of diversity bands for both large trees and the set of all trees along the basin. Given the performance of the RF models and the distribution of sampling sites in the basin, no inferences outside the main range of the sampled data and on other ecosystems are allowed. Therefore, our analysis of the distribution of tree diversity is restricted to the Brazilian Amazon basin.

While our analysis does not attempt explicitly to measure the possible impacts of climate change on large tree diversity, it is concerning to note that several climatic variables strongly associated with tree diversity may undergo intense changes under credible climate change scenarios. Climate-induced changes in the frequency of anomalous events, such as the increased occurrence of storms, the frequency of lightning and severe droughts, are already observed (Dale et al., 2001; Kamimura et al., 2022; Seidl et al., 2017). Changes in environmental variables associated with disturbances could have large negative impacts on the diversity and survival of large trees.

Given the enormous tree diversity of tropical forests, understanding the effects of climate change on diversity patterns is critical and should be analyzed as soon as possible at finer scales within Amazonia. Such knowledge is critical to refining conservation perspectives in a changing world—for example, to what extent are currently protected areas in Amazonia susceptible to climate disturbance-induced impacts on their biologically critical large trees? Efforts to understand how deforestation and climate change interact, and to mitigate their impacts, are urgently needed in light of the high and increasing rates of deforestation that have taken place in the Brazilian Amazon in recent years and which threaten the most extraordinary biodiversity on the planet.

AUTHOR CONTRIBUTIONS

Robson Borges de Lima conceived the main idea of the manuscript and accessed relevant Brazilian Amazon Plots in the ForestPlots.net database with the approval of data owners. Robson Borges de Lima and Eric Bastos Görgens led the compilation of field inventory and remote sensing data with the assistance of Cinthia Pereira de Oliveira, Diego Armando S. da Silva, Anderson Pedro B. Batista, Jadson Coelho de Abreu, and Rinaldo L. Caraciolo Ferreira. All co-authors contributed data. Robson Borges de Lima performed the analyses with the assistance of Eric Bastos Görgens. Robson Borges de Lima wrote the first draft of the manuscript, with all authors providing editorial input.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available at https://doi.org/10.5281/zenodo.7688243 (accessed on 05 July 2022).

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REFERENCES

Ali, A., Mattsson, E., & Nissanka, S. (2022). Big-sized trees and species-functional diversity pathways mediate divergent impacts of environmental factors on individual biomass variability in Sri Lankan tropical forests. *Journal of Environmental Management*, *315*, 115177. https://doi.org/10.1016/j.jenvman.2022.115177

Amaral, D. D., Carvalho, W. V., Costa Neto, S. V., Santos, J. U., Bastos, M. D., Amaral, L. T., & Gurgel, E. S. (2021). Floristic influence of Amazonian lowland dense rain Forest on the pioneer vegetation with marine influence, Restinga of Pará state, Brazil. *Rodriguésia*, *72*, e00532020. https://doi.org/10.1590/2175-7860202172093

Balvanera, P., & Aguirre, E. (2006). Tree diversity, environmental heterogeneity, and productivity in a Mexican tropical dry Forest1. *Biotropica*, *38*(4), 479–491. https://doi.org/10.1111/j.1744-7429.2006.00161.x

Barbier, N., Couteron, P., Proisy, C., Malhi, Y., & Gastellu-Etchegorry, J.-P. (2010). The variation of apparent crown size and canopy heterogeneity across lowland Amazonian forests: Amazon forest canopy properties. *Global Ecology and Biogeography*, *19*(1), 72–84. https://doi.org/10.1111/j.1466-8238.2009.00493.x

Baret, F., Weiss, M., Lacaze, R., Camacho, F., Makhmara, H., Pacholcyzk, P., & Smets, B. (2013). GEOV1: LAI and FAPAR essential climate variables and FCOVER global time series capitalizing over existing products. Part1: Principles of development and production. *Remote Sensing of Environment*, *137*, 299–309. https://doi.org/10.1016/j.rse.2012.12.027

Barkhordarian, A., Saatchi, S. S., Behrangi, A., Loikith, P. C., & Mechoso, C. R. (2019). A recent systematic increase in vapor pressure deficit over tropical South America. *Scientific Reports*, *9*(1), 15331. https://doi.org/10.1038/s41598-019-51857-8

Bastin, J., Rutishauser, E., Kellner, J. R., Saatchi, S., Pélissier, R., Hérault, B., Slik, F., Bogaert, J., De Cannière, C., Marshall, A. R., Poulsen, J., Alvarez-Loyayza, P., Andrade, A., Angbonga-Basia, A., Araujo-Murakami, A., Arroyo, L., Ayyappan, N., de Azevedo, C. P., Banki, O., … Zebaze, D. (2018). Pan-tropical prediction of forest structure from the largest trees. *Global Ecology and Biogeography*, *27*(11), 1366–1383. https://doi.org/10.1111/geb.12803

Beck, J., Brehm, G., & Fiedler, K. (2011). Links between the environment, abundance and diversity of Andean moths: Abundance and diversity of Andean moths. *Biotropica*, *43*(2), 208–217. https://doi.org/10.1111/j.1744-7429.2010.00689.x

Bennett, A. C., McDowell, N. G., Allen, C. D., & Anderson-Teixeira, K. J. (2015). Larger trees suffer most during drought in forests worldwide. *Nature Plants*, *1*(10), 1–5. https://doi.org/10.1038/nplants.2015.139

Berde, V., Chari, B., & Berde, C. (2020). *Wetland and biodiversity hotspot conservation*. Current State and Future Impacts of Climate Change on Biodiversity (pp. 144–153). https://doi.org/10.4018/978-1-7998-1226-5.ch009

Borges Silva, L. C., Pavão, D. C., Elias, R. B., Moura, M., Ventura, M. A., & Silva, L. (2022). Taxonomic, structural diversity and carbon stocks in a gradient of Island forests. *Scientific Reports*, *12*(1), 1038. https://doi.org/10.1038/s41598-022-05045-w

Bruijnzeel, L. A., Kappelle, M., Mulligan, M., & Scatena, F. N. (2011). Tropical montane cloud forests: State of knowledge and sustainability perspectives in a changing world. *Tropical Montane Cloud Forests: Science for Conservation and Management*, 691–740. https://doi.org/10.1017/CBO9780511778384.074

Cai, L., Kreft, H., Taylor, A., Denelle, P., Schrader, J., Essl, F., Van Kleunen, M., Pergl, J., Pyšek, P., Stein, A., Winter, M., Barcelona, J., Fuentes, N., Inderjit, Karger, D. N., Kartesz, J., Kuprijanov, A., Nishino, M., Nickrent, D., Nowak, A., … Weigelt, P. (2023). Global models and predictions of plant diversity based on advanced machine learning techniques. *New Phytologist*, *237*(4), 1432–1445. https://doi.org/10.1111/nph.18533

Carvalho, G. (2020). *flora: Tools for Interacting with the Brazilian Flora 2020* (0.3.4). https://CRAN.R-project.org/package=flora

Cazzolla Gatti, R., Reich, P. B., Gamarra, J. G. P., Crowther, T., Hui, C., Morera, A., Bastin, J.-F., de-Miguel, S., Nabuurs, G.-J., Svenning, J.-C., Serra-Diaz, J. M., Merow, C., Enquist, B., Kamenetsky, M., Lee, J., Zhu, J., Fang, J., Jacobs, D. F., Pijanowski, B., … Liang, J. (2022). The number of tree species on earth. *Proceedings of the National Academy of Sciences of the United Sates of America*, *119*(6), e2115329119. https://doi.org/10.1073/pnas.2115329119

Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T.-J. (2004). A new statistical approach for assessing similarity of species composition with incidence and abundance data: A new statistical approach for assessing similarity. *Ecology Letters*, *8*(2), 148–159. https://doi.org/10.1111/j.1461-0248.2004.00707.x

Clark, D. B., & Clark, D. A. (2000). Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management*, *137*(1), 185–198. https://doi.org/10.1016/S0378-1127(99)00327-8

13652486, 2023, 17, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.16821 by Oxford University, Wiley Online Library on [06/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Clark, D. B., Ferraz, A., Clark, D. A., Kellner, J. R., Letcher, S. G., & Saatchi, S. (2019). Diversity, distribution and dynamics of large trees across an old-growth lowland tropical rain forest landscape. *PLoS One*, *14*(11), e0224896. https://doi.org/10.1371/journal.pone.0224896

Clinebell, R., Phillips, O., Gentry, A., Stark, N., & Zuuring, H. (1995). Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation*, *4*, 56–90. https://doi.org/10.1007/BF00115314

Coelho de Souza, F., Dexter, K. G., Phillips, O. L., Pennington, R. T., Neves, D., Sullivan, M. J. P., Alvarez-Davila, E., Alves, Á., Amaral, I., Andrade, A., Aragao, L. E. O. C., Araujo-Murakami, A., Arets, E. J. M. M., Arroyo, L., Aymard C., G. A., Bánki, O., Baraloto, C., Barroso, J. G., Boot, R. G. A., … Baker, T. R. (2019). Evolutionary diversity is associated with wood productivity in Amazonian forests. *Nature Ecology & Evolution*, *3*(12), 1754–1761. https://doi.org/10.1038/s41559-019-1007-y

Colville, J. F., Beale, C. M., Forest, F., Altwegg, R., Huntley, B., & Cowling, R. M. (2020). Plant richness, turnover, and evolutionary diversity track gradients of stability and ecological opportunity in a megadiversity center. *Proceedings of the National Academy of Sciences of the United Sates of America*, *117*(33), 20027–20037. https://doi.org/10.1073/pnas.1915646117

Colwell, R. K., Chao, A., Gotelli, N. J., Lin, S.-Y., Mao, C. X., Chazdon, R. L., & Longino, J. T. (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology*, *5*(1), 3–21. https://doi.org/10.1093/jpe/rtr044

Craven, D., Filotas, E., Angers, V. A., & Messier, C. (2016). Evaluating resilience of tree communities in fragmented landscapes: Linking functional response diversity with landscape connectivity. *Diversity and Distributions*, *22*(5), 505–518. https://doi.org/10.1111/ddi.12423

Crowther, T. W., Glick, H. B., Covey, K. R., Bettigole, C., Maynard, D. S., Thomas, S. M., Smith, J. R., Hintler, G., Duguid, M. C., Amatulli, G., Tuanmu, M.-N., Jetz, W., Salas, C., Stam, C., Piotto, D., Tavani, R., Green, S., Bruce, G., Williams, S. J., … Bradford, M. A. (2015). Mapping tree density at a global scale. *Nature*, *525*(7568), 201–205. https://doi.org/10.1038/nature14967

Cutler, F. original by L. B. and A., & Wiener, R. port by A. L. and M. (2022). *randomForest: Breiman and Cutler's Random Forests for Classification and Regression* (4.7-1.1). https://CRAN.R-project.org/package=randomForest

Da Cunha, C., Barbosa, F., Costa, C., & Junk, W. (2021). *Woody encroachment and its control in periodically flooded grasslands of the pantanal, a large Brazilian wetland*. Flora and Vegetation of the Pantanal Wetland (pp. 491–512). https://doi.org/10.1007/978-3-030-83375-6_11

Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., Hanson, P. J., Irland, L. C., Lugo, A. E., Peterson, C. J., Simberloff, D., Swanson, F. J., Stocks, B. J., & Wotton, B. M. (2001). Climate change and forest disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *Bioscience*, *51*(9), 723–734. https://doi.org/10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2

de Lima, R. B., Görgens, E. B., Batista, A. P. B., da Silva, D. A. S., de Oliveira, C. P., & de Sousa, C. S. C. (2022). Diversity and big tree patterns in the Brazilian Amazon. *Diversity*, *14*(7), 503. https://doi.org/10.3390/d14070503

Draper, F. C., Costa, F. R. C., Arellano, G., Phillips, O. L., Duque, A., Macía, M. J., Ter Steege, H., Asner, G. P., Berenguer, E., Schietti, J., Socolar, J. B., de Souza, F. C., Dexter, K. G., Jørgensen, P. M., Tello, J. S., Magnusson, W. E., Baker, T. R., Castilho, C. V., Monteagudo-Mendoza, A., … Baraloto, C. (2021). Amazon tree dominance across forest strata. *Nature Ecology & Evolution*, *5*(6), 757–767. https://doi.org/10.1038/s41559-021-01418-y

Duivenvoorden, J. E. (1995). Tree species composition and rain forest-environment relationships in the middle Caquetá area, Colombia, NW Amazonia. *Vegetatio*, *120*(2), 91–113. https://doi.org/10.1007/BF00034341

Ehbrecht, M., Seidel, D., Annighöfer, P., Kreft, H., Köhler, M., Zemp, D. C., Puettmann, K., Nilus, R., Babweteera, F., Willim, K., Stiers, M., Soto, D., Boehmer, H. J., Fisichelli, N., Burnett, M., Juday, G., Stephens, S. L., & Ammer, C. (2021). Global patterns and climatic controls of forest structural complexity. *Nature Communications*, *12*(1), 519. https://doi.org/10.1038/s41467-020-20767-z

Esquivel Muelbert, A., Baker, T., Dexter, K., Lewis, S., Ter Steege, H., Lopez-Gonzalez, G., Monteagudo, A., Brienen, R., Feldpausch, T., Pitman, N., Alonso, A., van der Heijden, G., Peña-Claros, M., Ahuite, M., Alexiaides, M., Alvarez-Davila, E., Araujo-Murakami, A., Arroyo Padilla, L., Aulestia, M., & Valverde, F. (2016). Seasonal drought limits tree species across the neotropics. *Ecography*, *40*, 618–629. https://doi.org/10.1111/ecog.01904

Fagua, J. C., Jantz, P., Burns, P., Massey, R., Buitrago, J. Y., Saatchi, S., Hakkenberg, C., & Goetz, S. J. (2021). Mapping tree diversity in the tropical forest region of Chocó-Colombia. *Environmental Research Letters*, *16*(5), 054024. https://doi.org/10.1088/1748-9326/abf58a

Fauset, S., Johnson, M. O., Gloor, M., Baker, T. R., Monteagudo, M. A., Brienen, R. J. W., Feldpausch, T. R., Lopez-Gonzalez, G., Malhi, Y., Ter Steege, H., Pitman, N. C. A., Baraloto, C., Engel, J., Pétronelli, P., Andrade, A., Camargo, J. L. C., Laurance, S. G. W., Laurance, W. F., Chave, J., … Phillips, O. L. (2015). Hyperdominance in Amazonian forest carbon cycling. *Nature Communications*, *6*(1), 6857. https://doi.org/10.1038/ncomms7857

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Figueroa, S., & Nobre, C. (1990). Precipitation distribution over central and western tropical South America. *Climanálise*, *5*, 36–45.

Fisher, R. A., Corbet, A. S., & Williams, C. B. (1943). The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology*, *12*(1), 42–58. https://doi.org/10.2307/1411

ForestPlots.net, Blundo, C., Carilla, J., Grau, R., Malizia, A., Malizia, L., Osinaga-Acosta, O., Bird, M., Bradford, M., Catchpole, D., Ford, A., Graham, A., Hilbert, D., Kemp, J., Laurance, S., Laurance, W., Ishida, F. Y., Marshall, A., Waite, C., … Tran, H. D. (2021). Taking the pulse of Earth's tropical forests using networks of highly distributed plots. *Biological Conservation*, *260*, 108849. https://doi.org/10.1016/j.biocon.2020.108849

Householder, J. E., Schöngart, J., Piedade, M. T., Junk, W. J., Ter Steege, H., Montero, J. C., De Assis, R. L., de Aguiar, D. P., Pombo, M. M., Quaresma, A. C., & Demarchi, L. O. (2021). Modeling the ecological responses of tree species to the flood pulse of the Amazon Negro River floodplains. *Frontiers in Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.628606

Funk, C., Peterson, P., Landsfeld, M., Pedreros, D., Verdin, J., Shukla, S., Husak, G., Rowland, J., Harrison, L., Hoell, A., & Michaelsen, J. (2015). The climate hazards infrared precipitation with stations—A new environmental record for monitoring extremes. *Scientific Data*, *2*(1), 1–21. https://doi.org/10.1038/sdata.2015.66

Gastauer, M., Sarmento, P. S. D. M., Caldeira, C. F., Castro, A. F., Ramos, S. J., Trevelin, L. C., Jaffé, R., Rosa, G. A., Carneiro, M. A. C., Valadares, R. B. d. S., Oliveira, G., & Souza Filho, P. W. M. (2021). Shannon tree diversity is a surrogate for mineland rehabilitation status. *Ecological Indicators*, *130*, 108100. https://doi.org/10.1016/j.ecolind.2021.108100

Gentry, A. H. (1988). Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of Sciences of the United Sates of America*, *85*(1), 156–159. https://doi.org/10.1073/pnas.85.1.156

13652486, 2023, 17, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.16821 by Oxford University, Wiley Online Library on [06/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Gerstner, K., Moreno-Mateos, D., Gurevitch, J., Beckmann, M., Kambach, S., Jones, H. P., & Seppelt, R. (2017). Will your paper be used in a meta-analysis? Make the reach of your research broader and longer lasting. *Methods in Ecology and Evolution*, *8*(6), 777–784. https://doi.org/10.1111/2041-210X.12758

Gora, E. M., Bitzer, P. M., Burchfield, J. C., Gutierrez, C., & Yanoviak, S. P. (2021). The contributions of lightning to biomass turnover, gap formation and plant mortality in a tropical forest. *Ecology*, *102*(12), e03541. https://doi.org/10.1002/ecy.3541

Gora, E. M., Bitzer, P. M., Burchfield, J. C., Schnitzer, S. A., & Yanoviak, S. P. (2017). Effects of lightning on trees: A predictive model based on in situ electrical resistivity. *Ecology and Evolution*, *7*(20), 8523–8534. https://doi.org/10.1002/ece3.3347

Gora, E. M., Burchfield, J. C., Muller-Landau, H. C., Bitzer, P. M., & Yanoviak, S. P. (2020). Pantropical geography of lightning-caused disturbance and its implications for tropical forests. *Global Change Biology*, *26*(9), 5017–5026. https://doi.org/10.1111/gcb.15227

Gora, E. M., & Esquivel-Muelbert, A. (2021). Implications of size-dependent tree mortality for tropical forest carbon dynamics. *Nature Plants*, *7*(4), 384–391. https://doi.org/10.1038/s41477-021-00879-0

Gorgens, E. B., Nunes, M. H., Jackson, T., Coomes, D., Keller, M., Reis, C. R., Valbuena, R., Rosette, J., Almeida, D. R. A., Gimenez, B., Cantinho, R., Motta, A. Z., Assis, M., Souza Pereira, F. R., Spanner, G., Higuchi, N., & Ometto, J. P. (2021). Resource availability and disturbance shape maximum tree height across the Amazon. *Global Change Biology*, *27*(1), 177–189. https://doi.org/10.1111/gcb.15423

Green, J., Gentine, P., Berry, J., Zhang, Y., & Ciais, P. (2020). Amazon rainforest photosynthesis increases in response to atmospheric dryness. *Science Advances*, *6*, eabb7232. https://doi.org/10.1126/sciadv.abb7232

Guimaraes, A. F., de Souza, C. R., Rosa, C., dos Santos, J. P., Teixeira, L. A. F., Zanzini, L. P., Santiago, W. T. V., & da Silva Zanzini, A. C. (2021). Small-scale environmental variations drive vegetation structure and diversity in Amazon riverine forests. *Flora*, *283*, 151916. https://doi.org/10.1016/j.flora.2021.151916

Hall, J., Muscarella, R., Quebbeman, A., Arellano, G., Thompson, J., Zimmerman, J. K., & Uriarte, M. (2020). Hurricane-induced rainfall is a stronger predictor of tropical Forest damage in Puerto Rico than maximum wind speeds. *Scientific Reports*, *10*(1), 4318. https://doi.org/10.1038/s41598-020-61164-2

Harris, D. J., Ndolo Ebika, S. T., Sanz, C. M., Madingou, M. P. N., & Morgan, D. B. (2021). Large trees in tropical rain forests require big plots. *Plants, People, Planet*, *3*(3), 282–294. https://doi.org/10.1002/ppp3.10194

Hengl, T., de Jesus, J. M., Heuvelink, G. B. M., Gonzalez, M. R., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M. N., Geng, X., Bauer-Marschallinger, B., Guevara, M. A., Vargas, R., MacMillan, R. A., Batjes, N. H., Leenaars, J. G. B., Ribeiro, E., Wheeler, I., Mantel, S., & Kempen, B. (2017). SoilGrids250m: Global gridded soil information based on machine learning. *PLoS One*, *12*(2), e0169748. https://doi.org/10.1371/journal.pone.0169748

Hofhansl, F., Chacón-Madrigal, E., Fuchslueger, L., Jenking, D., Morera Beita, A., Plutzar, C., Silla, F., Andersen, K., Buchs, D., Dullinger, S., Fiedler, K., Franklin, O., Hietz, P., Huber, W., Quesada, C., Rammig, A., Schrodt, F., Vincent, A., Weissenhofer, A., & Wanek, W. (2020). Climatic and edaphic controls over tropical forest diversity and vegetation carbon storage. *Scientific Reports*, *10*, 5066. https://doi.org/10.1038/s41598-020-61868-5

Homeier, J., & Leuschner, C. (2021). Factors controlling the productivity of tropical Andean forests: Climate and soil are more important than tree diversity. *Biogeosciences*, *18*(4), 1525–1541. https://doi.org/10.5194/bg-18-1525-2021

Hsieh, T. C., Chao, K. H. M., & Chao, A. (2022). *iNEXT: Interpolation and Extrapolation for Species Diversity*. (3.0.0). https://CRAN.R-project.org/package=iNEXT

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*(12), 1451–1456. https://doi.org/10.1111/2041-210X.12613

Jiang, M., Felzer, B. S., Nielsen, U. N., Medlyn, B. E., & Fortin, M. (2017). Biome-specific climatic space defined by temperature and precipitation predictability. *Global Ecology and Biogeography*, *26*(11), 1270–1282. https://doi.org/10.1111/geb.12635

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*(2), 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Jost, L. (2007). Partitioning diversity into independent alpha and Beta components. *Ecology*, *88*(10), 2427–2439. https://doi.org/10.1890/06-1736.1

Joswig, J. S., Wirth, C., Schuman, M. C., Kattge, J., Reu, B., Wright, I. J., Sippel, S. D., Rüger, N., Richter, R., Schaepman, M. E., van Bodegom, P. M., Cornelissen, J. H. C., Díaz, S., Hattingh, W. N., Kramer, K., Lens, F., Niinemets, Ü., Reich, P. B., Reichstein, M., … Mahecha, M. D. (2022). Climatic and soil factors explain the two-dimensional spectrum of global plant trait variation. *Nature Ecology & Evolution*, *6*, 36–50. https://doi.org/10.1038/s41559-021-01616-8

Junk, W., Brown, M., Campbell, I., Finlayson, M., Ramberg, L., & Warner, B. (2006). The comparative biodiversity of seven globally important wetlands: A synthesis. *Aquatic Sciences*, *68*, 400–414. https://doi.org/10.1007/s00027-006-0856-z

Junk, W., Piedade, M. T., Schöngart, J., Wittmann, F., & Da Cunha, C. (2018). Brazilian wetlands: Classification. In *The wetland book: I: Structure and function, management, and methods*. The Wetland Book (pp. 1569–1575). https://doi.org/10.1007/978-90-481-9659-3_333

Kamimura, K., Nanko, K., Matsumoto, A., Ueno, S., Gardiner, J., & Gardiner, B. (2022). Tree dynamic response and survival in a category-5 tropical cyclone: The case of super typhoon Trami. *Science Advances*, *8*(10), eabm7891. https://doi.org/10.1126/sciadv.abm7891

Kearsley, E., Hufkens, K., Verbeeck, H., Bauters, M., Beeckman, H., Boeckx, P., & Huygens, D. (2019). Large-sized rare tree species contribute disproportionately to functional diversity in resource acquisition in African tropical forest. *Ecology and Evolution*, *9*(8), 4349–4361. https://doi.org/10.1002/ece3.4836

Keeley, A. T. H., Beier, P., & Jenness, J. S. (2021). Connectivity metrics for conservation planning and monitoring. *Biological Conservation*, *255*, 109008. https://doi.org/10.1016/j.biocon.2021.109008

Keil, P., & Chase, J. M. (2019). Global patterns and drivers of tree diversity integrated across a continuum of spatial grains. *Nature Ecology & Evolution*, *3*(3), 390–399. https://doi.org/10.1038/s41559-019-0799-0

Kindt, R. (2022). *BiodiversityR: Package for community ecology and suitability analysis*. (2.14–4). https://CRAN.R-project.org/package=BiodiversityR

Kling, M., & Ackerly, D. (2021). Global wind patterns shape genetic differentiation, asymmetric gene flow, and genetic diversity in trees. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, e2017317118. https://doi.org/10.1073/pnas.2017317118

Kraft, N., Comita, L., Chase, J., Sanders, N., Swenson, N., Crist, T., Stegen, J., Vellend, M., Boyle, B., Anderson, M., Cornell, H., Davies, K., Freestone, A., Inouye, B., Harrison, S., & Myers, J. (2011). Disentangling the drivers of diversity along latitudinal and elevational gradients. *Science (New York, N.Y.)*, *333*, 1755–1758. https://doi.org/10.1126/science.1208584

Laurance, W., & Curran, T. (2008). Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. *Austral Ecology*, *33*, 399–408. https://doi.org/10.1111/j.1442-9993.2008.01895.x

Liang, J., Gamarra, J. G. P., Picard, N., Zhou, M., Pijanowski, B., Jacobs, D. F., Reich, P. B., Crowther, T. W., Nabuurs, G. J., de-Miguel, S., Fang, J., Woodall, C. W., Svenning, J. C., Jucker, T., Bastin, J. F., Wiser, S. K., Slik, F., Hérault, B., Alberti, G., … Hui, C. (2022). Co-limitation towards lower latitudes shapes global forest diversity

13652486, 2023, 17, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.16821 by Oxford University, Wiley Online Library on [06/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

gradients. *Nature Ecology and Evolution*, *6*, 1423–1437. https://doi.org/10.1038/s41559-022-01831-x

Lindenmayer, D. B. (2017). Conserving large old trees as small natural features. *Biological Conservation*, *211*, 51–59. https://doi.org/10.1016/j.biocon.2016.11.012

Lindenmayer, D. B., & Laurance, W. F. (2016). The unique challenges of conserving large old trees. *Trends in Ecology & Evolution*, *31*(6), 416–418. https://doi.org/10.1016/j.tree.2016.03.003

Liu, J., Lindenmayer, D. B., Yang, W., Ren, Y., Campbell, M. J., Wu, C., Luo, Y., Zhong, L., & Yu, M. (2019). Diversity and density patterns of large old trees in China. *Science of the Total Environment*, *655*, 255–262. https://doi.org/10.1016/j.scitotenv.2018.11.147

Maharjan, S., Sterck, F., Raes, N., & Poorter, L. (2021). Temperature and soils predict the distribution of plant species along the Himalayan elevational gradient. *Journal of Tropical Ecology*, *1–13*, 58–70. https://doi.org/10.1017/S026646742100050X

Marca-Zevallos, M. J., Moulatlet, G. M., Sousa, T. R., Schietti, J., de Souza Coelho, L., Ramos, J. F., de Andrade Lima Filho, D., Amaral, I. L., de Almeida Matos, F. D., Rincón, L. M., Cardenas Revilla, J. D., Pansonato, M. P., Gribel, R., Barbosa, E. M., Miranda, I. P., de Matos Bonates, L. C., Guevara, J. E., Salomão, R. P., Ferreira, L. V., … Costa, F. R. C. (2022). Local hydrological conditions influence tree diversity and composition across the Amazon basin. *Ecography*, *2022*. https://doi.org/10.1111/ecog.06125

Marques, M., Swaine, M. D., & Liebsch, D. (2011). Diversity distribution and floristic differentiation of the coastal lowland vegetation: Implications for the conservation of the Brazilian Atlantic Forest. *Biodiversity and Conservation*, *20*, 153–168. https://doi.org/10.1007/s10531-010-9952-4

Marra, D. M., Chambers, J. Q., Higuchi, N., Trumbore, S. E., Ribeiro, G. H. P. M., Dos Santos, J., Negrón-Juárez, R. I., Reu, B., & Wirth, C. (2014). Large-scale wind disturbances promote tree diversity in a Central Amazon forest. *PLoS One*, *9*(8), e103711. https://doi.org/10.1371/journal.pone.0103711

Mendieta-Leiva, G., Buckley, H. L., & Zotz, G. (2022). Directional changes over time in the species composition of tropical vascular epiphyte assemblages. *Journal of Ecology*, *110*(3), 553–568. https://doi.org/10.1111/1365-2745.13817

Meyer, H., & Pebesma, E. (2022). Machine learning-based global maps of ecological variables and the challenge of assessing them. *Nature Communications*, *13*, 2208. https://doi.org/10.1038/s41467-022-29838-9

Mitchell, S. J. (2013). Wind as a natural disturbance agent in forests: A synthesis. *Forestry*, *86*(2), 147–157. https://doi.org/10.1093/forestry/cps058

Moraes, R. M., Correa, S. B., Rodrigues Da Costa Doria, C., Duponchelle, F., Miranda, G., Montoya, M., Phillips, O. L., Salinas, N., Silman, M., Ulloa Ulloa, C., Zapata-Ríos, G., Arieira, J., & Ter Steege, H. (2021). Chapter 4: Amazonian ecosystems and their ecological functions. In C. Nobre, A. Encalada, E. Anderson, F. H. Roca Alcazar, M. Bustamante, C. Mena, M. Peña-Claros, G. Poveda, J. P. Rodriguez, S. Saleska, S. E. Trumbore, A. Val, L. Villa Nova, R. Abramovay, A. Alencar, A. C. Rodriguez Alzza, D. Armenteras, P. Artaxo, S. Athayde, … G. Zapata–Ríos (Eds.), *Amazon assessment report 2021* (1st ed.). UN Sustainable Development Solutions Network (SDSN). https://doi.org/10.55161/IKRT9380

Morrone, J. (2014). Biogeographical regionalisation of the Neotropical region. *Zootaxa*, *3782*, 1–10. https://doi.org/10.11646/zootaxa.3782.1.1

Nanda, S. A., Haq, M., Singh, S. P., Reshi, Z. A., Rawal, R. S., Kumar, D., Bisht, K., Upadhyay, S., Upreti, D. K., & Pandey, A. (2021). Species richness and β-diversity patterns of macrolichens along elevation gradients across the Himalayan arc. *Scientific Reports*, *11*(1), 20155. https://doi.org/10.1038/s41598-021-99675-1

Neves, D. M., Dexter, K. G., Baker, T. R., Coelho de Souza, F., Oliveira-Filho, A. T., Queiroz, L. P., Lima, H. C., Simon, M. F., Lewis, G. P., Segovia, R. A., Arroyo, L., Reynel, C., Marcelo-Peña, J. L., Huamantupa-Chuquimaco, I., Villarroel, D., Parada, G. A., Daza, A., Linares-Palomino, R., Ferreira, L. V., … Pennington, R. T. (2020). Evolutionary diversity in tropical tree communities peaks at intermediate precipitation. *Scientific Reports*, *10*, 1188. https://doi.org/10.1038/s41598-019-55621-w

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M. D., Durand, S., … Weedon, J. (2022). *vegan: Community Ecology Package* (2.6–4). https://CRAN.R-project.org/package=vegan

R Core Team. (2022). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Rau, E.-P., Gardiner, B. A., Fischer, F. J., Maréchaux, I., Joetzjer, E., Sun, I.-F., & Chave, J. (2022). Wind speed controls Forest structure in a subtropical Forest exposed to cyclones: A case study using an individual-based model. *Frontiers in Forests and Global Change*, *5*, 753100. https://doi.org/10.3389/ffgc.2022.753100

Rifai, S. W., Urquiza Muñoz, J. D., Negrón-Juárez, R. I., Ramírez Arévalo, F. R., Tello-Espinoza, R., Vanderwel, M. C., Lichstein, J. W., Chambers, J. Q., & Bohlman, S. A. (2016). Landscape-scale consequences of differential tree mortality from catastrophic wind disturbance in the Amazon. *Ecological Applications*, *26*(7), 2225–2237. https://doi.org/10.1002/eap.1368

Ripley, B., Venables, B., Bates, D. M. (ca 1998), Hornik K. (partial port, ca 1998), Gebhardt, A. (partial port), & Firth, D. (2022). *MASS: Support Functions and Datasets for Venables and Ripley's MASS* (7.3–58.1). https://CRAN.R-project.org/package=MASS

Roswell, M., Dushoff, J., & Winfree, R. (2021). A conceptual guide to measuring species diversity. *Oikos*, *130*(3), 321–338. https://doi.org/10.1111/oik.07202

Roy, K., Goldberg, E. E., & Harrison, S. E. S. (2007). Origination, extinction, and dispersal: Integrative models for understanding present-day diversity gradients. *The American Naturalist*, *170*(S2), S71–S85. https://doi.org/10.1086/519403

Sabatini, F. M., Jiménez-Alfaro, B., Jandt, U., Chytrý, M., Field, R., Kessler, M., Lenoir, J., Schrodt, F., Wiser, S. K., Arfin Khan, M. A. S., Attorre, F., Cayuela, L., De Sanctis, M., Dengler, J., Haider, S., Hatim, M. Z., Indreica, A., Jansen, F., Pauchard, A., … Bruelheide, H. (2022). Global patterns of vascular plant alpha diversity. *Nature Communications*, *13*(1), 4683. https://doi.org/10.1038/s41467-022-32063-z

Schmit, C., Rounsevell, M., & La Jeunesse, I. (2006). The limitations of spatial land use data in environmental analysis. *Environmental Science & Policy*, *9*, 174–188. https://doi.org/10.1016/j.envsci.2005.11.006

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, *7*, 395–402. https://doi.org/10.1038/nclimate3303

Silman, M., Bush, M., & Flenley, J. (2007). *Plant species diversity in Amazonian forests*. Plant species diversity in Amazonian forests (pp. 269–294). https://doi.org/10.1007/978-3-540-48842-2_10

Silveira, F. A. O., Negreiros, D., Barbosa, N. P. U., Buisson, E., Carmo, F. F., Carstensen, D. W., Conceição, A. A., Cornelissen, T. G., Echternacht, L., Fernandes, G. W., Garcia, Q. S., Guerra, T. J., Jacobi, C. M., Lemos-Filho, J. P., Le Stradic, S., Morellato, L. P. C., Neves, F. S., Oliveira, R. S., Schaefer, C. E., … Lambers, H. (2016). Ecology and evolution of plant diversity in the endangered campo rupestre: A neglected conservation priority. *Plant and Soil*, *403*(1), 129–152. https://doi.org/10.1007/s11104-015-2637-8

Slik, J. W. F., Arroyo-Rodríguez, V., Aiba, S.-I., Alvarez-Loayza, P., Alves, L. F., Ashton, P., Balvanera, P., Bastian, M. L., Bellingham, P. J.,

13652486, 2023, 17, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.16821 by Oxford University, Wiley Online Library on [06/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

van den Berg, E., Bernacci, L., da Conceição Bispo, P., Blanc, L., Böhning-Gaese, K., Boeckx, P., Bongers, F., Boyle, B., Bradford, M., Brearley, F. Q., … Venticinque, E. M. (2015). An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(24), 7472–7477. https://doi.org/10.1073/pnas.1423147112

Slik, J. W. F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J.-L., Eler, E., Ferreira, L., Forshed, O., Fredriksson, G., Gillet, J.-F., … Zweifel, N. (2013). Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics: Large trees and tropical forest biomass. *Global Ecology and Biogeography*, *22*(12), 1261–1271. https://doi.org/10.1111/geb.12092

Slik, J. W. F., Raes, N., Aiba, S.-I., Brearley, F. Q., Cannon, C. H., Meijaard, E., Nagamasu, H., Nilus, R., Paoli, G., Poulsen, A. D., Sheil, D., Suzuki, E., Van Valkenburg, J. L. C. H., Webb, C. O., Wilkie, P., & Wulffraat, S. (2009). Environmental correlates for tropical tree diversity and distribution patterns in Borneo. *Diversity and Distributions*, *15*(3), 523–532. https://doi.org/10.1111/j.1472-4642.2009.00557.x

Song, X., Cao, M., Li, J., Kitching, R., Nakamura, A., Laidlaw, M., Tang, Y., Sun, Z., Zhang, W., & Yang, J. (2021). Different environmental factors drive tree species diversity along elevation gradients in three climatic zones in Yunnan, southern China. *Plant Diversity*, *43*, 433–443. https://doi.org/10.1016/j.pld.2021.04.006

Sullivan, M., Lewis, S., Affum-Baffoe, K., Castilho, C., Costa, F., cuni sanchez, A., Ewango, C., Hubau, W., Marimon, B., Monteagudo, A., Qie, L., Sonké, B., Vásquez Martínez, R., Baker, T., Brienen, R., Feldpausch, T., Galbraith, D., Gloor, M., Malhi, Y., & Phillips, O. (2020). Long-term thermal sensitivity of Earth's tropical forests. *Science*, *368*(6493), 869–874.

Syfert, M. M., Brummitt, N. A., Coomes, D. A., Bystriakova, N., & Smith, M. J. (2018). Inferring diversity patterns along an elevation gradient from stacked SDMs: A case study on Mesoamerican ferns. *Global Ecology and Conservation*, *16*, e00433. https://doi.org/10.1016/j.gecco.2018.e00433

Tallents, L. A., Lovett, J. C., Hall, J. B., & Hamilton, A. C. (2005). Phylogenetic diversity of forest trees in the Usambara mountains of Tanzania: Correlations with altitude. *Botanical Journal of the Linnean Society*, *149*(2), 217–228. https://doi.org/10.1111/j.1095-8339.2005.00431.x

Ter Steege, H., Pitman, N., Sabatier, D., Baraloto, C., Salomão, R., Guevara Andino, J., Phillips, O., Castilho, C., Magnusson, W., Molino, J.-F., Monteagudo, A., Vargas, P., Montero, J., Feldpausch, T., Honorio Coronado, E., Killeen, T., Mostacedo, B., Vásquez Martínez, R., Assis, R., & Silman, M. (2013). Hyperdominance in the Amazonian tree Flora. *Science (New York, N.Y.)*, *342*, 1243092. https://doi.org/10.1126/science.1243092

Ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., Van Der Hout, P., Daly, D. C., Silveira, M., Phillips, O., Vasquez, R., Van Andel, T., Duivenvoorden, J., De Oliveira, A. A., Ek, R., Lilwah, R., Thomas, R., Van Essen, J., Baider, C., Maas, P., Mori, S., … Morawetz, W. (2003). A spatial model of tree α-diversity and tree density for the Amazon. *Biodiversity and Conservation*, *12*(11), 2255–2277. https://doi.org/10.1023/A:1024593414624

Ter Steege, H., Vaessen, R. W., Cárdenas-López, D., Sabatier, D., Antonelli, A., de Oliveira, S. M., Pitman, N. C. A., Jørgensen, P. M., & Salomão, R. P. (2016). The discovery of the Amazonian tree flora with an updated checklist of all known tree taxa. *Scientific Reports*, *6*(1), 29549. https://doi.org/10.1038/srep29549

Terra, M. D., Santos, R. M., Prado Júnior, J. A., de Mello, J. M., Scolforo, J. R. S., Fontes, M. A. L., Schiavini, I., Dos Reis, A. A., Bueno, I. T., Magnago, L. F. S., & Ter Steege, H. (2018). Water availability drives gradients of tree diversity, structure and functional traits in the Atlantic–Cerrado–caatinga transition, Brazil. *Journal of Plant Ecology*, *11*(6), 803–814. https://doi.org/10.1093/jpe/rty017

Tolmos, M. L., Kreft, H., Ramirez, J., Ospina, R., & Craven, D. (2022). Water and energy availability mediate biodiversity patterns along an elevational gradient in the tropical Andes. *Journal of Biogeography*, *49*, 712–726. https://doi.org/10.1111/jbi.14332

Venter, M., Dwyer, J., Dieleman, W., Ramachandra, A., Gillieson, D., Laurance, S., Cernusak, L. A., Beehler, B., Jensen, R., & Bird, M. I. (2017). Optimal climate for large trees at high elevations drives patterns of biomass in remote forests of Papua New Guinea. *Global Change Biology*, *23*(11), 4873–4883. https://doi.org/10.1111/gcb.13741

Wagner, F. H., Hérault, B., Bonal, D., Stahl, C., Anderson, L. O., Baker, T. R., Becker, G. S., Beeckman, H., Boanerges Souza, D., Botosso, P. C., Bowman, D. M. J. S., Bräuning, A., Brede, B., Brown, F. I., Camarero, J. J., Camargo, P. B., Cardoso, F. C. G., Carvalho, F. A., Castro, W., … Aragão, L. E. O. C. (2016). Climate seasonality limits leaf carbon assimilation and wood productivity in tropical forests. *Biogeosciences*, *13*(8), 2537–2562. https://doi.org/10.5194/bg-13-2537-2016

White, P. S., & Pickett, S. T. A. (1985). Chapter 1—Natural disturbance and patch dynamics: An introduction. In S. T. A. Pickett & P. S. White (Eds.), *The ecology of natural disturbance and patch dynamics* (pp. 3–13). Academic Press. https://doi.org/10.1016/B978-0-08-050495-7.50006-5

Wilson, A. M., & Jetz, W. (2016). Remotely sensed high-resolution global cloud dynamics for predicting ecosystem and biodiversity distributions. *PLoS Biology*, *14*(3), e1002415. https://doi.org/10.1371/journal.pbio.1002415

Wittmann, F., Schongart, J., Montero, J. C., Motzer, T., Junk, W. J., Piedade, M. T. F., Queiroz, H. L., & Worbes, M. (2006). Tree species composition and diversity gradients in white-water forests across the Amazon Basin. *Journal of Biogeography*, *33*(8), 1334–1347. https://doi.org/10.1111/j.1365-2699.2006.01495.x

Yanoviak, S. P., Gora, E. M., Bitzer, P. M., Burchfield, J. C., Muller-Landau, H. C., Detto, M., Paton, S., & Hubbell, S. P. (2020). Lightning is a major cause of large tree mortality in a lowland neotropical forest. *New Phytologist*, *225*(5), 1936–1944. https://doi.org/10.1111/nph.16260

Zelený, D., Li, C.-F., & Chytrý, M. (2010). Pattern of local plant species richness along a gradient of landscape topographical heterogeneity: Result of spatial mass effect or environmental shift? *Ecography*, *33*(3), 578–589.

Zheng, X., Fu, J., Ramamonjisoa, N., Zhu, W., He, C., & Lu, C. (2019). Relationship between wetland plant communities and environmental factors in the Tumen River basin in Northeast China. *Sustainability*, *11*(6), Article 6. https://doi.org/10.3390/su11061559

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