

Functional biogeography of Neotropical moist forests: Trait–climate relationships and assembly patterns of tree communities

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Abstract

Aim: Here we examine the functional profile of regional tree species pools across the latitudinal distribution of Neotropical moist forests, and test trait–climate relationships among local communities. We expected opportunistic strategies (acquisitive traits, small seeds) to be overrepresented in species pools further from the equator, but also in terms of abundance in local communities in currently wetter, warmer and more seasonal climates.

Location: Neotropics.

Time period: Recent.

Major taxa studied: Trees.

Methods: We obtained abundance data from 471 plots across nine Neotropical regions, including c. 100,000 trees of 3,417 species, in addition to six functional traits. We compared occurrence-based trait distributions among regional species pools, and evaluated single trait–climate relationships across local communities using community abundance-weighted means (CWMs). Multivariate trait–climate relationships were assessed by a double-constrained correspondence analysis that tests both how CWMs relate to climate and how species distributions, parameterized by niche centroids in climate space, relate to their traits.

Results: Regional species pools were undistinguished in functional terms, but opportunistic strategies dominated local communities further from the equator, particularly in the Northern Hemisphere. Climate explained up to 57% of the variation in CWM traits, with increasing prevalence of lower-statured, light-wooded and softer-leaved species bearing smaller seeds in more seasonal, wetter and warmer climates. Species distributions were significantly but weakly related to functional traits.

Main conclusions: Neotropical moist forest regions share similar sets of functional strategies, from which local assembly processes, driven by current climatic conditions, select for species with different functional strategies. We can thus expect functional responses to climate change driven by changes in relative abundances of species already present regionally. Particularly, equatorial forests holding the most conservative traits and large seeds are likely to experience the most severe changes if climate change triggers the proliferation of opportunistic tree species.

KEYWORDS

climate change, climate seasonality, community assembly, functional composition, functional traits, latitude, precipitation, species pool, temperature

1 | INTRODUCTION

Plants have evolved a broad range of functional strategies to cope with diverse environmental conditions (Díaz et al., 2016; Pierce et al., 2017). The functional assembly of plant communities results from the interplay

among eco-evolutionary forces operating at different spatio-temporal scales (Kraft & Ackerly, 2014). At regional scales, the diverse functional strategies found in any given species pool reflect long-term speciation, dispersal and extinction filters (Mittelbach & Schemske, 2015). For instance, long-term climatic instability and natural disturbance regimes,

such as hurricanes, storms and forest expansion–retraction dynamics due to glacial cycles, may select for functional profiles that favour population persistence under unstable conditions, while disturbance-sensitive species may be rare or even absent from regions under such conditions (Balmford, 1996; Betts et al., 2019). At local scales, the functional profile of plant communities depends on the filtering of regionally available species across varying current climate regimes (Cadotte & Tucker, 2017; Swenson et al., 2012). Assessing changes in functional composition of regional species pools and local communities along wide (bio)geographic and climatic gradients can help to understand potential responses to climate change and other human-caused disturbances (Violle et al., 2014). For instance, global climate change will soon bring unprecedented extreme climates to the Neotropics (Mora et al., 2013). Therefore, assessing how tree communities are functionally structured by trait–climate relationships helps predict the future of Neotropical forests in a rapidly changing world.

The advent of global plant trait databases in recent decades has enabled numerous investigations of patterns of trait variation and their relationships with climatic and biogeographic gradients (e.g. Swenson et al., 2012). These studies have revealed intriguing patterns, such as the tendency of plant species in warmer and less seasonal sites (closer to the equator) to be taller and bear larger and softer leaves, larger seeds and denser woods (Moles et al., 2007, 2009; Swenson et al., 2012; Wright et al., 2004, 2017). However, these large-scale trait patterns were described mostly from species occurrence data across spatial grid-cells or latitudinal bands, and therefore failed to account for ecological processes operating at local scales that govern abundance of species and ultimately the functional profile of plant assemblages. Moreover, studies that have assessed variation in abundance of species and their traits in local communities are based on either a single regional flora (e.g. van der Sande et al., 2016) or a single trait (e.g. Swenson & Enquist, 2007), and thus are unable to capture species assembly processes along wide biogeographic and climatic gradients. Scaling up abundance-based analyses of local communities to biogeographic scales can improve our understanding about climatic effects on local trait dominance, which ultimately drives ecosystem functioning (Poorter et al., 2017). In this way, Bruelheide et al. (2018) recently used a large dataset to examine global trait–environment relationships at the local community level (including abundance data), and found only weak support ($R^2 < .1$) for trait–climate relationships. These global-scale analyses, though insightful, can mask relevant patterns within biotas that share a relatively common (but diverse) biogeographic history, such as Neotropical moist forests.

Neotropical moist forests extend from southern Mexico to northern Argentina and represent an enormous variation in past and current climatic conditions (Blonder et al., 2018; Frierson et al., 2013) and biogeographic histories (Burnham & Graham, 1999; Gentry, 1982). Overall, these differences clearly result in distinct taxonomic and phylogenetic composition more or less packed into biogeographic provinces. For instance, tropical moist forests of Meso-America (including Mexico) are taxonomically distinct from those in South America; the flora of the latter being mostly of Gondwanan origin while the northern Neotropics supports many plant lineages with

Laurasian affinity (Gentry, 1982; Graham, 1999). Also, palynological evidence points to a higher frequency of past disturbance events and faster recovery of tropical forests in northern Central America compared to South American counterparts (Cole et al., 2014). Mexican forests are the northern limit of the Neotropical forest distribution and experienced repeated expansion–retraction cycles due to Pleistocene glaciations (Burnham & Graham, 1999; Graham, 1999), compared to South America, where many large blocks of forests remained stable during the last glacial and the influence of the Andes and the South American dry diagonal corridor is remarkable (Colinvaux et al., 2000; Hoorn et al., 2010; Leite et al., 2016).

While assessing relationships between traits and current climate is straightforward, addressing the effects of biogeographic history is challenging. Historical contingencies such as speciation/extinction dynamics and dispersal events must have affected the functional structure of current species pools and different drivers might act across localities (Fukami, 2015). Distance from the equator is related to current climate seasonality but has also been used as a proxy of biogeographic history, from plants to mammals, given its correlation to past cycles of climate change (Betts et al., 2019; Dynesius & Jansson, 2000). It is thus reasonable to expect that tropical biotas far from the equator experienced, currently and in the past, more shifting climates than their equatorial counterparts (Betts et al., 2019; Blonder et al., 2018). Such instability might select for opportunistic strategies related to fast growth and high dispersal ability. For instance, northern forests are mostly composed of broad-ranged plant species due to short- and long-term climatic instability, while small-ranged species concentrate under stable climates in Central America, Amazonia and Atlantic forests (Morueta-Holme et al., 2013), which are relatively equatorial regions that also support higher phylogenetic endemism (Sandel et al., 2020). In contrast, extreme southern Neotropical vegetation has developed under relatively low and seasonal temperature and precipitation levels (Oliveira-Filho et al., 2013). The extent to which such historical contingencies can induce distinct signatures on the functional composition of Neotropical moist forests is yet to be fully understood.

Several key aspects of community functional composition can be expressed through the 'global spectrum of plant form and function' (Díaz et al., 2016). Specifically, plants well adapted to resource-poor/stressful environments with low disturbance regimes tend to grow slowly (i.e. low metabolic resource demand) and invest in dense, durable tissues (i.e. conservative traits). In contrast, acquisitive resource-use traits (e.g. low-density woods, soft leaves) favour hydraulic efficiency and rapid plant growth, allowing resource pre-emption in productive habitats such as those under wetter and warmer climates (Reich, 2014; Westoby et al., 2002). This opportunistic strategy can also benefit under more seasonal climates by optimizing carbon gain during the growing season in the more open forests that allow more light to reach the understorey (Kikuzawa et al., 2013; Kobe, 1999). Regarding size-related traits, increasing leaf area favours light capture, but limits heat exchange with the surrounding air, and leads to higher daytime transpirational water loss, thereby being favoured in warm, moist and sunny environments

(Wright et al., 2017). Also, larger seeds may promote higher seedling performance under low resource availability (Leishman & Westoby, 1994; Muller-Landau, 2010), while smaller-seeded species have greater seed output that favours dispersal to recently disturbed sites and seeds that are more likely to exhibit dormancy, which favours survival under variable climates (de Casas et al., 2017). Finally, larger trees tend to have greater access to light and belowground resources, but are more prone to hydraulic failure during drought (Brum et al., 2019). Combinations of these traits define ecological strategies that influence plant responses to environmental conditions (Grime & Pierce, 2012).

Here we test two mutually compatible effects of biogeographic history and current climate as structuring drivers of the functional organization of tree communities across Neotropical moist forests. If historical contingency prevails, then we should expect functional dissimilarities among regional tree species pools, which could lead to differences in functional composition of local communities occurring in similar climates in different regions. If current climate represents a prevailing force, functional differences should emerge at the local scale due to changes in trait dominance in response to climatic conditions. In particular, we expected that regional species pools should be composed of different sets of functional strategies, with higher prevalence of species with opportunistic ecological strategies (i.e. low-density tissues, small seeds) in regions further from the equator due to long-term instability that selects for fast growth and high dispersal ability. Across local communities, more seasonal, wetter and warmer climates should favour dominance of opportunistic strategies. We additionally assessed the consistency of trait–climate relationships by evaluating to what extent the distribution of species, expressed as the abundance-weighted mean climatic conditions where they are found (i.e. niche centroids), is mediated by functional traits. We discuss our results in terms of how useful they are for the understanding of both community assembly patterns and potential responses of Neotropical tree floras to climate change and anthropogenic disturbances in human-dominated landscapes.

2 | METHODS

2.1 | Study regions and plots

We studied 471 forest plots from nine biogeographic regions distributed across the Neotropics, covering the whole latitudinal distribution of Neotropical moist forests (Figure 1; see Supporting Information Table S1 for details on sampling across regions). All plots were located in lowland (up to 800 m a.s.l.), old-growth forests within a variable matrix of land uses. Mean annual precipitation ranged from 1,154 to 7,068 mm, and mean annual temperature from c. 17 to 28 °C (Supporting Information Figure S1). Temperature seasonality increases with distance from equator (Wright et al., 2009), while average temperature and precipitation are typically higher towards the northern Neotropics due to northward heat transport by ocean circulation (Frierson et al., 2013; Figure 1).

2.2 | Vegetation data

We used data from 96,290 live adult trees (stems with diameter at breast height, DBH ≥ 10 cm; excluding lianas and palms) belonging to 3,417 species. Tree inventories were carried out by the authors as described elsewhere (Arroyo-Rodríguez et al., 2009; Benchimol & Peres, 2015; Faria et al., 2009; Hernández-Ruedas et al., 2014; Orihuela et al., 2015; Pinho et al., 2018; Pitman et al., 2001; Santos et al., 2008) or compiled from the 'Salvias' database through the Botanical Information and Ecology Network ('BIEN') R package (Maitner et al., 2018), which includes the Gentry plots (Gentry, 1988). The sampled area and total number of individuals and species sampled by region are summarized in Supporting Information Table S1. The slight difference in sampling methods (e.g. plot sizes) should not affect our results as we focus on the *relative* dominance of functional traits and strategies within communities and the resulting variation across the Neotropics.

2.3 | Functional traits

A comprehensive set of six traits was measured in the field (following Pérez-Harguindeguy et al., 2013) and compiled from global databases, such as 'TRY Plant Trait Database' (Kattge et al., 2020) and the 'Seed Information Database' (SID; Royal Botanic Gardens Kew, 2020). These traits are leaf area (LA; cm^2), specific leaf area (SLA; cm^2/g), leaf dry matter content (LDMC; mg/g), wood density (WD; g/cm^3), seed mass (SM; mg) and maximum height (Hmax; m). We chose these traits because they are known to influence tree performance along climatic gradients (Reich, 2014; Westoby et al., 2002), and position species along the plant (and organ) economics and size-related traits spectra (Díaz et al., 2016; Pierce et al., 2017). For instance, the leaf and stem traits considered are expected to reflect a trade-off between rapid resource acquisition that enables growth in resource-rich environments (indicated by high SLA, low LDMC, low WD), and conservation of resources in well-protected tissues that ensure survival under low resource availability, indicated by the opposite traits (Reich, 2014).

For leaf traits in compound-leaved species, we considered leaflets as the sample unit. Although we recognize the importance of intraspecific trait variation in community assembly (Siefert et al., 2015), we used species' mean functional traits as we consider this a meaningful approach for the purpose of this study due to the extensive species-level trait data and high species turnover among regions. Species-level trait data covered on average from 57 to 80% of total plot abundances across traits/regions (see Supporting Information Table S2 for a summary of trait coverage by region). For species with doubtful identification and/or no trait information, we first used average trait values at the genus level, then we imputed remaining missing values (for which no genus-level data were available) through multivariate trait imputation with chained equations by predictive mean matching, using the R package 'mice' (van Buuren & Groothuis-Oudshoorn, 2011). The imputed trait data represented 3% or less of individuals in plots for 40 of the 54 region-trait combinations and over 10% for just one combination (see

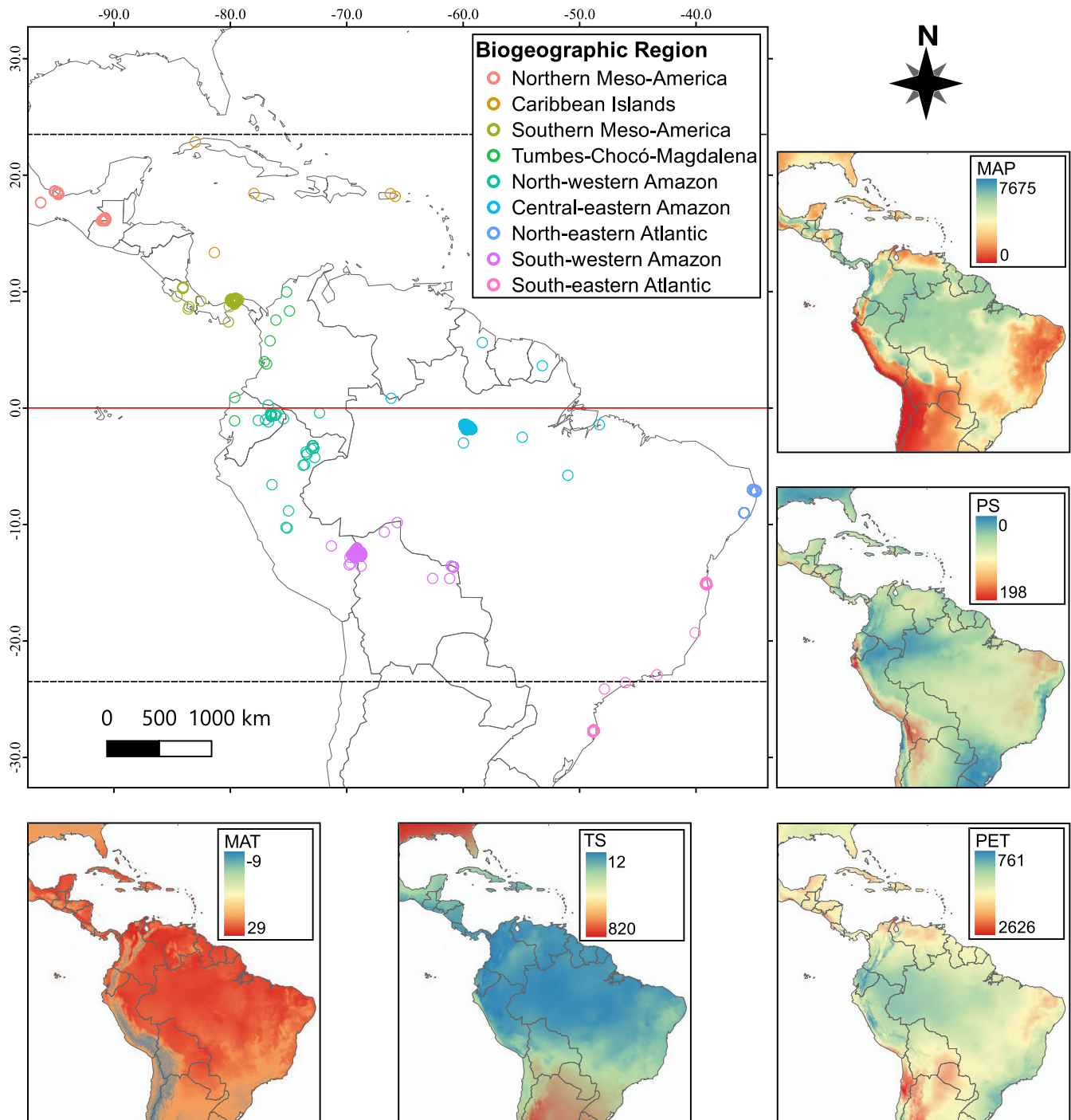


FIGURE 1 Location of the 471 forest plots studied in nine biogeographic regions, and variation in the five climatic variables considered throughout the Neotropics. MAP = mean annual precipitation (mm); MAT = mean annual temperature (°C); PS = precipitation seasonality (coefficient of variation of monthly precipitation values); TS = temperature seasonality (standard deviation of monthly temperature values); PET = potential evapotranspiration (mm)

Supporting Information Table S2 for a summary by region), and the distribution of the original and imputed datasets largely overlapped (Supporting Information Figure S2). Genus-level trait means were well correlated with species mean traits (Supporting Information Table S3), and their inclusion led to similar distributions of community abundance-weighted mean (CWM) trait values (Supporting Information Figure S3). These findings demonstrate that our results

are not due to spurious artefacts in the imputation of missing trait data. Also, the exclusion of trees with DBH < 10 cm should not represent a significant bias because adults covered the whole range of functional strategies evident among saplings, and abundance-weighted distributions of species trait values largely overlap when considering smaller trees (see example for Northern Meso-America, Supporting Information Figure S4).

2.4 | Climate data

For each plot, we assessed the average of five key bioclimatic variables that are thought to drive trait distributions and vegetation patterns (Moles, 2018; Swenson et al., 2012). The five climatic variables are mean annual precipitation (MAP), mean annual temperature (MAT), precipitation seasonality (PS; coefficient of variation of monthly values), temperature seasonality (TS; standard deviation of monthly values, multiplied by 100) and potential evapotranspiration (PET; the amount of water expected to be removed by the atmosphere through evapotranspiration processes annually). The first four variables were obtained from WorldClim version 2.0 (Fick & Hijmans, 2017), which is a high-resolution global geo-database (30 arc seconds or c. 1 km at equator) of monthly average data from 1970 to 2000. The PET was calculated from a set of WorldClim variables (taken in the same timeframe as above), using an equation proposed by the Food and Agriculture Organization of the United Nations, which involves minimum, maximum and average temperature, solar radiation, wind speed and water vapour pressure (Trabucco & Zomer, 2018). Other climatic variables were considered but then excluded due to collinearity (see below, Supporting Information Table S4). The five climatic variables considered were weakly inter-correlated (Supporting Information Table S4), but were strongly related to latitude (i.e. south–north gradient) or degrees from equator (Supporting Information Figure S1). Despite complex climate variability due to, for example, ocean circulation and elevation (Frierson et al., 2013), in this dataset temperature seasonality was strongly positively correlated with degrees from equator, while other climatic variables (MAP, MAT, PET, PS) increased linearly from south to north (Supporting Information Figure S1, see Figure 1 for the overall climatic pattern across the Neotropics).

2.5 | Data analyses

We log-transformed LA, SLA and SM values, and square root (sqrt)-transformed Hmax to reduce skewness in trait distributions. We also log-transformed MAP to reduce the influence of two exceptionally wet sites. Functional composition of regional species pools was described from distributions of the traits of species occurring in each region. Functional traits were scaled-up from the species level to the plot level by calculating the CWM (i.e. species' trait values weighted by their relative abundances), which reflects the dominance of trait values in a community (Muscarella et al., 2017). CWM trait values were calculated using function 'functcomp' from the 'FD' R package (Laliberté & Legendre, 2010). To examine trait covariation patterns among species and communities, we applied principal component analyses (PCAs) to the species and CWM trait matrices, using the 'prcomp' R function (Venables & Ripley, 2002). We also computed CWM of species scores on the first two principal component axes, which should reflect economics and size trade-offs in functional strategies (Díaz et al., 2016).

To assess changes in community functional composition in response to climate or geography, we constructed separate linear

mixed-effects models for the CWM of each functional trait or strategy (i.e. species scores on the PCA axes, see above). The fixed effects were either the five bioclimatic variables described above or the geographic variables, latitude (to describe south-to-north gradients) and degrees from equator (to describe gradients toward higher latitudes in both hemispheres). The random effect 'biogeographic region' was included in all models to account for the nested structure of our sampling design, and to assess among-region variation not explained by latitude or climate. To avoid multicollinearity between climatic or geographic variables, we checked the variance inflation factor of each predictor in each model, using the 'car' package for R. All values were < 3, which allowed us to include all five climate variables or the two geographic variables in the models (Neter et al., 1996). After running a full model with each set of predictors (i.e. climatic and geographic variables) for each response variable (i.e. CWM of each trait and PCA axes scores) using the maximum likelihood method with the R package 'lme4' (Bates et al., 2015), we tested all possible combinations of predictors and performed a model selection procedure to select the best-fit models as those with lowest Akaike information criterion values ($\Delta\text{AICc} < 2$). Then, we applied model averaging to make inferences on how individual climatic variables influence CWM of traits and strategies, using the 'MuMin' R package (Barton, 2014).

To assess the variance in CWM of traits and strategies (i.e. species scores on principal component axes, see above) among regions and the strength of their relationships with latitude or climate, we partitioned the R^2 of each selected model into the total variance between regions ('conditional R^2 ') and the component explained by climate or latitude ('marginal R^2 '; Nakagawa & Schielzeth, 2013), reporting the variance explained by the model with highest marginal R^2 for each response variable. The difference between conditional and marginal R^2 values represents the variance between regions not explained by climate/latitude (expressed as fraction of the total variance). The within-region component is the remaining unexplained variance (i.e. $1 - \text{conditional } R^2$). For this, we used the R package 'piecewiseSEM' (Lefcheck, 2016). All the above-mentioned analyses were performed in R 4.0.4 (R Core Team, 2021).

To assess composite trait–climate relationships at both species and community level, we applied double-constrained correspondence analysis (dc-CA; ter Braak et al., 2018). The dc-CA method is a new and powerful regression-based approach, similar to the covariance-based three-table ordination RLQ method used to assess multivariate trait–environment relationships in what is known as the fourth-corner problem (Dray & Legendre, 2008). Like RLQ, dc-CA uses three data tables (trait values of species, environmental conditions of sites, and abundances of species per site) to define the correlation between traits and environmental conditions (i.e. the fourth-corner correlation). The fourth-corner correlation has proved to be powerful to test trait–environment relationships (Peres-Neto et al., 2017; ter Braak, 2017). dc-CA searches for linear combinations of traits and environmental variables that maximize their fourth-corner correlation, using weighted least-squares, where the weights for species and for sites are their total abundance. In contrast, RLQ maximizes covariance not correlation. By maximizing

the fourth-corner correlation, dc-CA considers the influence of environmental conditions on community functional composition (i.e. CWM traits) in combination with how species (environmental) niche centroids (SNC) relate to their traits (ter Braak et al., 2018). SNCs represent the mean climatic conditions where species are found (weighted by abundances) and are related to species' traits to discover whether trait-mediated mechanisms influence species' distributions. Specifically, the SNC with respect to environmental variable e is a weighted mean, calculated as $u_j = \sum_{i=1}^n y_{ij} e_i / \sum_{i=1}^n y_{ij}$, where y_{ij} refers to the abundance of the j^{th} species in the i^{th} site, and e_i is the value of the environmental variable at the i^{th} site.

We additionally applied dc-CA considering geographic gradients (latitude, longitude and degrees from equator) instead of climate variables as predictors, and performed variation partitioning to define the separate and shared effects of geographic and climatic gradients. We used the dc-CA based max-test to check significance of the dc-CA axes (ter Braak, 2017). The max-test solves the problem of inflated type I error rate in the fourth-corner approach (Peres-Neto et al., 2017) by applying two independent permutations for testing species- (SNC ~ traits) and community-level (CWM ~ climate) patterns, and selecting the highest p -value. We applied the max-test after aggregating plots separated by less than 50 km (Supporting Information Figure S5) to avoid pseudo-replication caused by nearby plots. In the analyses using dc-CA, the issue of the two exceptionally wet sites was solved by replacing their MAP values with the value 4,500 mm/year, slightly higher than the maximum in the dataset; this gave a slightly higher fit than the log-transformation, but did not give qualitatively different results. We performed the dc-CA using the software CANOCO 5.12 (ter Braak & Šmilauer, 2018).

3 | RESULTS

3.1 | Functional composition of Neotropical moist forest regions

The functional composition of tree species pools largely overlapped across regions (Figure 2a), but strong differences among regions emerged from abundance-weighted trait values at the local community level (i.e. CWM) (Figure 2b). Tree communities in forests near the equator (e.g. Amazonia, north-eastern Atlantic forest) were dominated by taller species with larger seeds, harder woods and greater leaf dry matter content. Tree communities in regions further from the equator were dominated by lower-statured species with smaller seeds and lower LDMC, particularly in the Northern Hemisphere (Figure 2b). CWM values of wood density and maximum height were, however, relatively high in the extreme south (i.e. south-eastern Atlantic forests), where specific leaf area achieved the lowest values (Figure 2b).

The first two PC axes of species-level trait values captured 55% of the variation in the functional space composed by six traits (Figure 3a). The first PC axis indicated a common spectrum of variation among economic and regenerative traits, varying from species with acquisitive traits (i.e. high SLA, low LDMC and WD) and small seeds (i.e. opportunistic strategies), to species with more conservative strategies (i.e. low SLA, high LDMC and WD) and larger seeds (Figure 3a, Supporting Information Table S5). The second axis mainly reflects variation in leaf area and maximum height, which covaried positively (Figure 3a, Supporting Information Table S5). Variation in SLA was mostly captured by a third PC axis (Supporting Information Table S5).

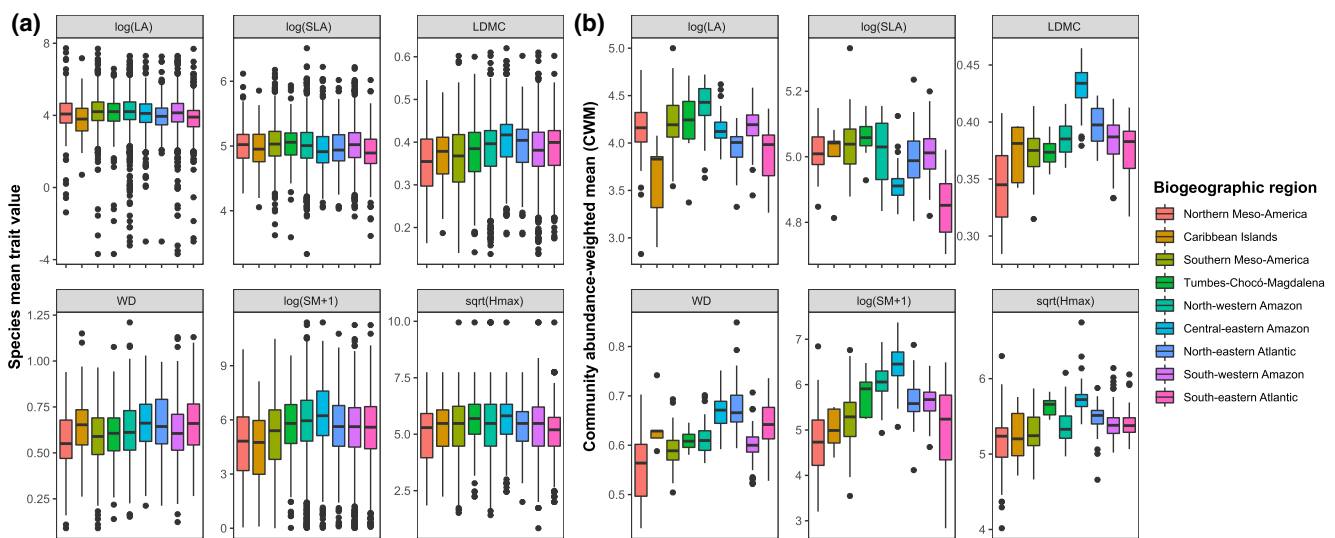


FIGURE 2 Differences between regions in functional trait values of (a) species present in each regional species pool (unweighted by abundance), and (b) the communities (i.e. abundance-weighted means – CWM) in each region, for 3,417 tree species distributed in 471 forest plots across nine Neotropical moist forest regions. Boxplots indicate the median (centre line), 25–75% quartiles (box edges), < 1.5 times the interquartile range (whiskers), and extreme values (dots). The boxplots are organized from the northernmost (left) to the southernmost region (right) along the distribution of the Neotropical moist forest biome. LA = leaf area (cm^2); SLA = specific leaf area (cm^2/g); LDMC = leaf dry matter content (g/g); WD = wood density (g/cm^3); SM = seed mass (mg); Hmax = maximum height (m); sqrt = square root

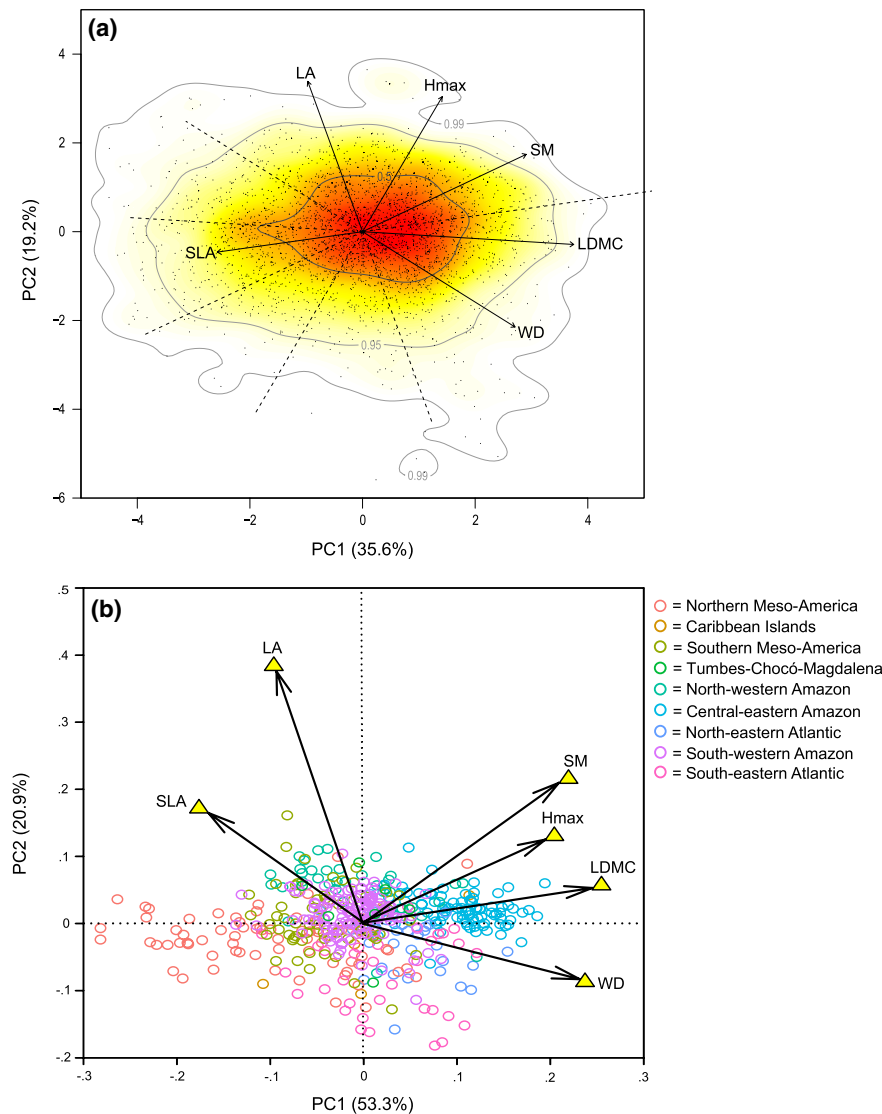


FIGURE 3 Ordination diagram of the first two axes of the principal component analysis (PCA) of (a) Neotropical tree species trait values ($n = 3,417$ species); and (b) community-weighted mean trait values of tree communities ($n = 471$ plots) distributed across nine Neotropical moist forest regions. The occurrence probability of species in the trait space is illustrated in (a) by colour gradients from highest (red) to lowest (white) kernel density, with contour lines indicating .5, .95 and .99 quantiles. LA = leaf area; SLA = specific leaf area; LDMC = leaf dry matter content; WD = wood density; SM = seed mass; Hmax = maximum height

The first two principal components of community-level trait values (i.e. CWM) captured more variation (74%) and revealed similar trade-offs (Figure 3b), except maximum height was strongly related to the first PC axis (Supporting Information Table S5). Tree communities from different regions could be distinguished along the first two PC axes (Figure 3b). Specifically, the first axis indicated a gradient from communities dominated by species with conservative traits (high WD and LDMC) in equatorial regions and in the extreme south of the Neotropical forest biome, to a more acquisitive (high SLA) community composition in northern forests. In turn, the second community trait axis distinguished communities in the south-eastern Atlantic region and Caribbean Islands as dominated by species with smaller leaves compared to more equatorial forests, particularly those across North-western Amazon and southern Meso-America (Figure 3b).

3.2 | Trait-climate relationships across Neotropical tree communities

Current climate explained 16 to 57% of the variation in CWM trait values across Neotropical moist forests (Table 1a, Figure 4). Temperature

seasonality presented the strongest relationships with CWM traits, except for leaf area, which was more strongly related to mean annual precipitation, and SLA, which was not responsive to climate variation (Table 1a). LDMC, SM, WD and Hmax decreased with increasing temperature seasonality, while mean annual temperature had similar (but much weaker) effects on the last three of these traits (Table 1a). Additionally, increasing annual precipitation was associated with increased dominance of tree species with lower wood density, larger organs and lower leaf dry matter content, while precipitation seasonality was negatively related to seed mass (Table 1a). The species functional strategies evident on the first two PC axes (Figure 3a) also changed predictably in response to climatic variables (Table 1b): PC1 (acquisitive to conservative resource economy) was strongly negatively related to temperature seasonality, while PC2 (small to large plants and organs) increased mainly with mean annual precipitation (Figure 4).

The first two dc-CA axes revealed significant (max-test, $p = .001$) composite trait-climate relationships (Figure 5, Supporting Information Table S6). The first axis describes a gradient from environments with relatively high seasonality in temperature and precipitation, combined with high annual precipitation and potential evapotranspiration, to less seasonal climates, along which there

TABLE 1 Results of averaging of the best-fitted mixed-effects models ($\Delta AIC_c < 2$) analysing the effects of climatic variables on the abundance-weighted community mean of (a) functional traits and (b) functional strategies, across 471 forest plots in nine biogeographic regions distributed throughout the Neotropics (see Figure 1)

			95% CI			
Model factors	β	SE	Lower	Upper	p-value	Models R ² (marginal/ conditional)
(a) Functional traits						
Log [leaf area (cm ²)]						.24/.29
Mean annual precipitation (MAP)	0.096	0.017	0.062	0.130	< 2e ⁻¹⁶	
Potential evapotranspiration (PET)	-0.124	0.024	-0.171	-0.076	4.00e ⁻⁰⁷	
Mean annual temperature (MAT)	0.059	0.026	0.008	0.109	.023	
Precipitation seasonality (PS)	0.043	0.028	0.015	0.092	.126	
Temperature seasonality (TS)	0.024	0.031	-0.016	0.102	.443	
Log [specific leaf area (cm ² /g)]						.09/.32
MAP	0.010	0.007	0.000	0.024	.160	
MAT	0.010	0.007	-0.001	0.025	.155	
PS	0.010	0.010	0.000	0.030	.284	
PET	-0.001	0.005	-0.029	0.011	.795	
TS	-0.003	0.007	-0.030	0.009	.695	
Leaf dry matter content (g/g)						.47/.70
TS	-0.025	0.003	-0.031	-0.020	< 2e ⁻¹⁶	
MAP	-0.003	0.002	-0.006	0.000	.026	
MAT	-0.003	0.003	-0.008	0.000	.224	
PET	-0.002	0.003	-0.010	0.003	.576	
PS	0.0001	0.001	-0.005	0.004	.894	
Log [seed mass (mg) + 1]						.57/.68
TS	-0.653	0.067	-0.783	-0.522	< 2e ⁻¹⁶	
MAT	-0.161	0.056	-0.270	-0.051	.003	
PS	-0.107	0.047	-0.188	-0.016	.022	
PET	-0.032	0.058	-0.220	0.035	.577	
MAP	-0.003	0.017	-0.088	0.062	.869	
Wood density (g/cm ³)						.39/.62
TS	-0.052	0.006	-0.064	-0.040	< 2e ⁻¹⁶	
MAP	-0.018	0.003	-0.024	-0.011	3.00e ⁻⁰⁷	
MAT	-0.016	0.005	-0.026	-0.005	.003	
PET	0.009	0.007	0.000	0.024	.207	
PS	-0.003	0.005	-0.016	0.001	.523	
Square root (sqrt) [maximum height (m)]						.16/.41
TS	-0.190	0.034	-0.256	-0.125	< 2e ⁻¹⁶	
MAT	-0.173	0.033	-0.239	-0.108	2.00e ⁻⁰⁷	
PET	0.057	0.045	0.005	0.145	.204	
PS	-0.004	0.014	-0.065	0.030	.767	
(b) Functional strategies						
Principal component 1 (PC1; economics spectrum)						.40/.69
MAP	-0.096	0.032	0.034	0.158	.002	
MAT	-0.159	0.043	0.075	0.243	.0002	
TS	-0.560	0.057	0.448	0.673	< 2e ⁻¹⁶	

(Continues)

TABLE 1 (Continued)

Model factors	β	SE	95% CI		p-value	Models R^2 (marginal/conditional)
			Lower	Upper		
PS	-0.017	0.035	-0.033	0.140	.634	.28/.28
PET	0.013	0.037	-0.174	0.068	.739	
PC2 (size spectrum)						
MAP	0.120	0.013	-0.145	-0.094	$< 2e^{-16}$	
PET	-0.125	0.017	0.092	0.158	$< 2e^{-16}$	
PS	0.060	0.015	-0.090	-0.031	$7.15e^{-05}$	
TS	-0.024	0.021	0.001	0.068	.255	
MAT	0.022	0.023	-0.073	0.002	.325	

Note: For each variable retained in a best-fit model, we indicate the mean coefficient (β), the standard error (SE), the 95% confidence intervals (95% CI) and the p -value. p -values of significant variables (according to 95% CI) are in bold. The predictors were standardized and thus the coefficients indicate their relative contribution for each response variable. The marginal R^2 (variance explained by climatic factors) and conditional R^2 (the former plus additional among-regions variance not explained by climatic factors) values of the full model are also shown. Units of climatic variables: MAP (mm), PET (mm), MAT ($^{\circ}\text{C}$), PS (coefficient of variation of monthly values), TS (standard deviation of monthly values multiplied by 100). ΔAICc refers to differences (delta) in corrected Akaike information criterion.

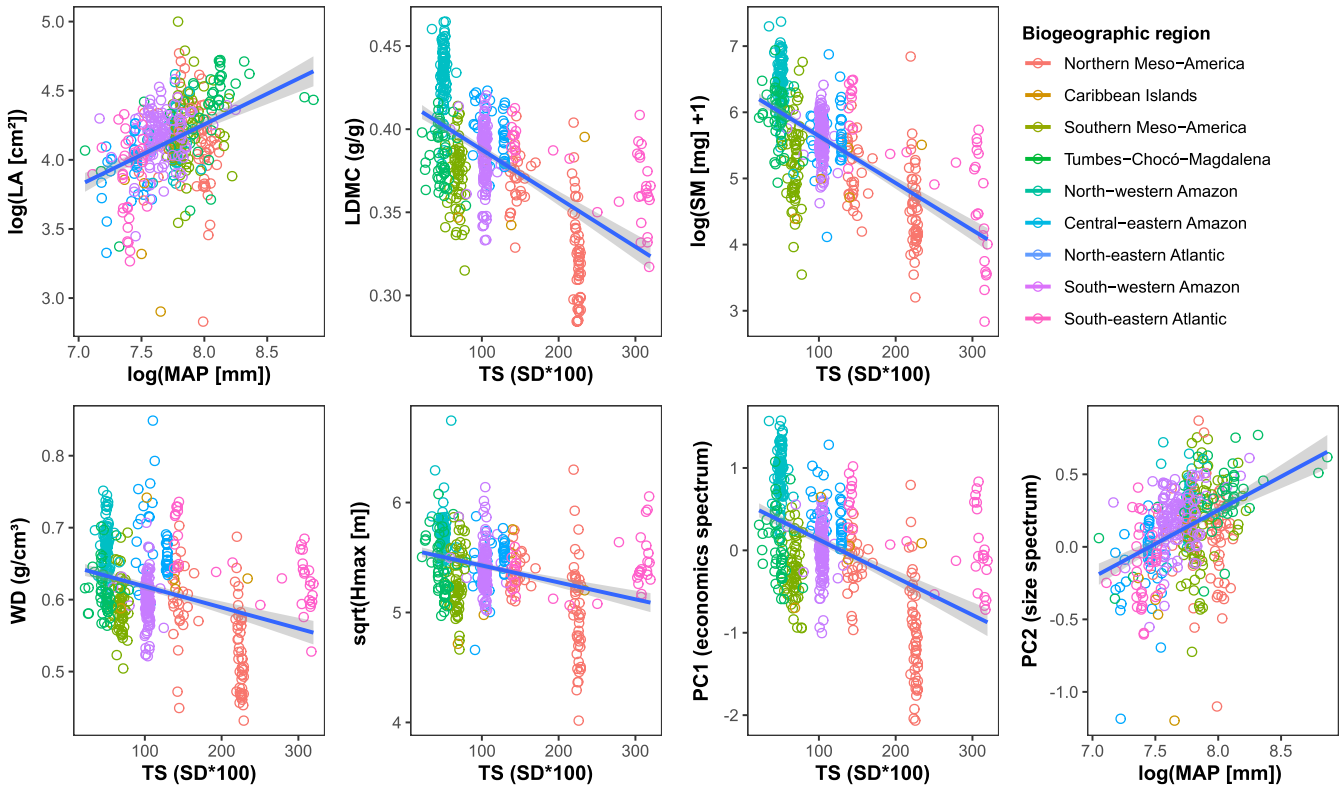


FIGURE 4 Significant relationships between climatic variables and community abundance-weighted mean (CWM) of functional traits and strategies [i.e. species scores on the two first axes of the principal component analysis (PCA) on functional traits, see Figure 3a], for 471 tree communities distributed across nine Neotropical moist forest regions (see Table 1 for details on the best models). LA = leaf area; LDMC = leaf dry matter content; WD = wood density; SM = seed mass; Hmax = maximum height; MAP = mean annual precipitation; TS = temperature seasonality; SD = standard deviation; sqrt = square root. The relationship with highest slope (i.e. estimate) is shown for each trait/strategy, except for LA and PC2, for which we selected the relationship with the lowest error and p -value from two relationships with similar slopes

was a shift in dominance from shorter plants with relatively acquisitive traits and small seeds, to slow-growing species with conservative traits and large seeds (Figure 5a). This first axis separated communities across northern regions from those in more equatorial regions (Figure 5b). The second dc-CA axis was mostly explained by variation in MAP and PET, reflecting a gradient from drier sites

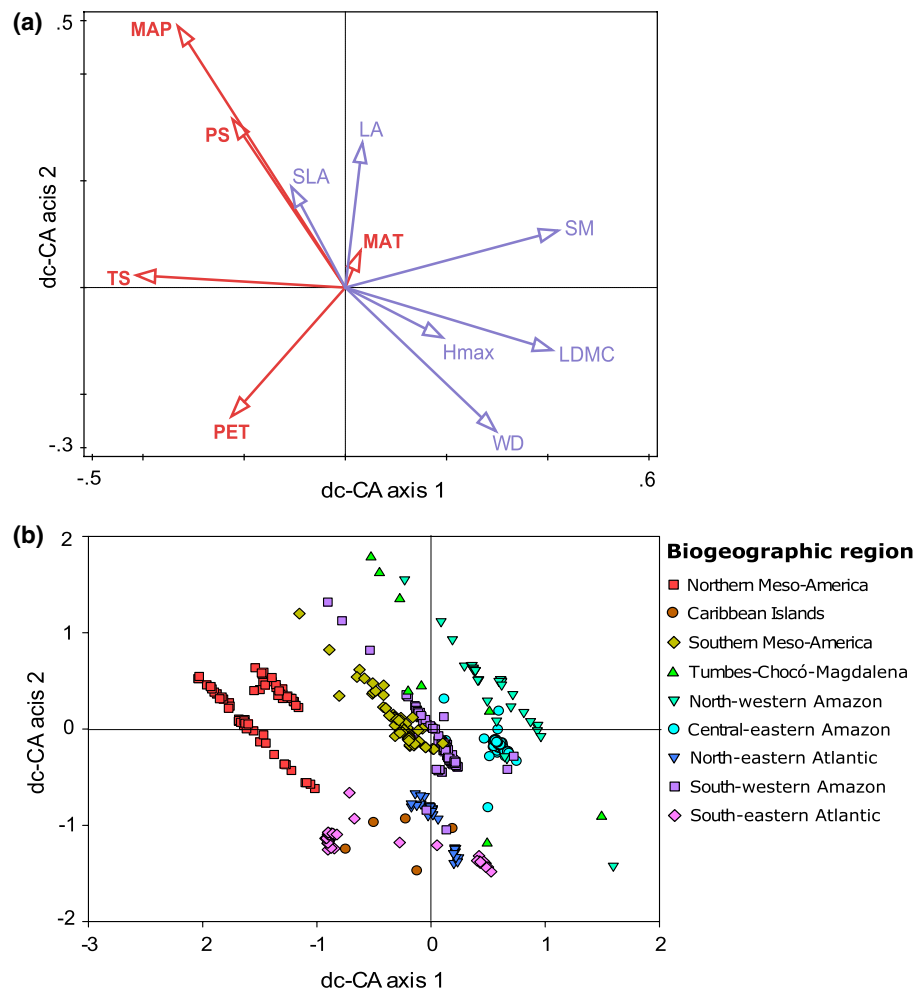


FIGURE 5 Ordination diagrams from double-constrained correspondence analysis (dc-CA) for 3,417 species across 471 Neotropical moist forest plots, showing (a) biplot of canonical weights of climate variables and scaled correlations of traits summarizing the coefficients of the multiple regressions of all community abundance-weighted means (CWMs) of traits on the climate predictors; and (b) position (constrained scores) of samples (plots) in the dc-CA biplot. Graphs (a) and (b) form a biplot of the CWMs of all plots and traits. The significance of dc-CA results was tested by aggregating community data by spatial clusters of plots ($n = 59$; see Supporting Information Figure S5) to avoid pseudo-replication (see Table 2 for related statistics). The position of the 30 species that contribute most to the first two dc-CA axes is shown in Supporting Information Figure S8. LA = leaf area; SLA = specific leaf area; LDMC = leaf dry matter content; WD = wood density; SM = seed mass; Hmax = maximum height; MAP = mean annual precipitation; MAT = mean annual temperature; TS = temperature seasonality; PS = precipitation seasonality; PET = potential evapotranspiration

under high potential evapotranspiration to exceptionally wet sites (Figure 5a). This second gradient explained the variation in dominance from small-leaved species with high woody density across south-eastern Atlantic forests and Caribbean Islands, to large-leaved, soft-wooded species in communities across northern regions, particularly the Chocó bioregion and north-western Amazon (Figure 5b).

Climate variables were good predictors of taxonomic composition across communities (CCA eigenvalues of .8 and .7 for the first two axes), as well as of multivariate gradients in community abundance-weighted traits (46% of variance explained; Supporting Information Table S6). In turn, traits were weak predictors of the distribution of individual species abundances across communities, explaining only 4% of variation in species climate niche centroids

(Supporting Information Table S6). Forward selection on climate variables revealed that three of the five climate variables (MAP, TS and PET) account for most variation in composite trait-climate gradients (Supporting Information Figure S6).

3.3 | Geographic gradients in community functional composition

All community-weighted mean traits were significantly related to either latitude or degrees from equator. LA, LDMC, WD and SM decreased with increasing degrees from equator, while SLA increased and Hmax decreased with latitude (i.e. from southern to northern forests; Supporting Information Figure S7). Latitude was more strongly

Component	Variation (adj. R^2)	% of explained	df	Mean square	F	p
Climate (unique)	.15	22.7	5	0.03	5.9	.0005
Geography (unique)	.12	17.8	3	0.04	7.2	.0045
Shared	.39	59.5	–	–	–	–
Total explained	.66	100	8	0.09	15.3	.0005

Note: The trait-structured variation is a weighted variance of the community abundance-weighted means (CWMs) with respect to orthonormalized traits with the sample total as weight.

TABLE 2 Variation partitioning of the trait-structured variation in the double-constrained correspondence analysis (dc-CA) with all traits, showing the unique and shared effects of geography (latitude, longitude, and degrees from equator) and climate [mean annual precipitation (MAP), mean annual temperature (MAT), temperature seasonality (TS), precipitation seasonality (PS), potential evapotranspiration (PET)] in aggregated samples of tree communities across Neotropical moist forests ($n = 59$; see Supporting Information Figure S5)

related to vegetation patterns (i.e. taxonomic turnover across communities), while degrees from equator explained relatively more of the functional variation (Supporting Information Table S7). Variance partitioning revealed unique and shared effects of geography and climate, combining to explain 66% of the variation in CWM trait values (Table 2). Most of this explained variation (39%) resulted from shared effects of geographic gradients and climate variables, though there were also unique effects of similar size from both climate (15%) and geography (12%) (Table 2).

4 | DISCUSSION

Species pools of Neotropical moist forest regions from southern Mexico to southern Brazil possess similar distributions of trait values. Long-term filters that can control for the functional composition of regional species pools thus have little to no importance. In contrast, local tree communities are functionally structured along climatic and (bio)geographic gradients. Species assembly processes that govern local abundance of species in tree communities must have generated the documented functional dissimilarities. The novelty of our findings is that we found clear though complex trait-climate relationships across Neotropical moist forests, that are not simply driven by geography. The observed patterns suggest an increase in relative abundance of lower-statured, light-wooded and softer-leaved species bearing smaller seeds (i.e. opportunistic strategies) under more seasonal climates in communities further away from the equator, especially under wetter and warmer conditions across northern forests. In contrast, communities in more stable climates (mostly close to the equator) are dominated by species with large seeds and conservative traits (i.e. the typical functional profile of late-successional tree species). Trait-climate relationships at the species level (i.e. species niche centroids ~ traits) were also significant but weaker, suggesting either that changes in the abundance of dominant species are responsible for varying functional signatures across Neotropical forests, or that there is scope for improvement of the trait set. It is important to recognize that dominance of functional strategies differs between regions mainly due to local assembly processes related to climate rather than changes in species pools

that would be the result of biogeographic history. This helps to understand how Neotropical forests may respond to climate change and other human-imposed disturbances.

Our results contrast with those of Bruelheide et al. (2018), in which functional composition of plant communities (abundance-based) was weakly related to climate at the global scale. At the continental/biome scale (i.e. within Neotropics), we found strong trait-climate relationships across Neotropical moist forest tree communities, with combinations of climatic variables explaining up to 57% of variance in CWM trait values. Changes in trait dominance were mainly driven by the increase in temperature seasonality with distance from the equator and, to a lesser extent, by changes in precipitation regimes, average temperature and potential evapotranspiration (Table 1) that are less clear in geographic terms (Figure 1). Slightly different from our findings, previous assessments of global trait distributions suggest that higher mean annual temperature and/or precipitation in equatorial regions leads to increased prevalence of conservative traits and larger seeds (e.g. Bruelheide et al., 2018; Moles et al., 2014; Swenson et al., 2012). This discrepancy may arise because global patterns of trait distribution may reflect major differences among predominant biomes across climatic zones. Also, global-scale studies usually include both woody and herbaceous species (e.g. Bruelheide et al., 2018), which respond differently to climate across the Neotropics (Šimová et al., 2018). Most importantly, global-scale studies include dry forests, where the combination of high temperatures with low and highly seasonal precipitation may represent a physical stress, favouring conservative strategies (Westoby et al., 2002). As our study focuses on Neotropical moist forests, higher temperatures and precipitation should actually favour acquisitive traits of trees, as we found, due for example to increased hydraulic efficiency (Santiago et al., 2018; Zhang et al., 2013). Our findings strengthen the notion that climatic conditions play a key role in trait filtering across Neotropical tree assemblages.

Despite differences in magnitude of climate effects, the direction of community-level trait-climate relationships (i.e. including abundance data) in the Neotropics generally agrees with that of species-level global trait-climate relationships (e.g. Swenson et al., 2012; Wright et al., 2017, see Moles, 2018 for a review of

these relationships). For example, we found that seed mass tends to be lower in plants growing at more seasonal sites further from the equator, as observed elsewhere (Malhado et al., 2015; Moles et al., 2007; Swenson et al., 2012), presumably because larger seeds require longer growing seasons for development and are less likely to exhibit dormancy, which helps seeds to survive under adverse seasonal conditions (de Casas et al., 2017; Thompson et al., 1993). Moreover, tree species in wetter sites tend to present larger leaves and softer wood and leaf tissues, as we found, because these traits maximize resource capture in productive environments (Westoby et al., 2002; Wright et al., 2017). Conversely, small leaves with low SLA characterize cold tolerance (Poorter et al., 2009; Wright et al., 2017) as we observed in the south-eastern Atlantic forests, a region that experiences relatively low and seasonal temperatures (Supporting Information Figure S1; Oliveira-Filho et al., 2013). Also in agreement with our findings, plant height tends to be limited under more seasonal climates (Moles et al., 2009; Swenson et al., 2012), and non-significant relationships between SLA and climatic gradients are more a rule than an exception (Moles, 2018). Finally, large seeds and conservative traits may provide advantages for species in shaded conditions of relatively closed-canopy forests near the equator (Kitajima & Poorter, 2010; Leishman & Westoby, 1994).

While the trait-climate relationships we observed are well supported by theory, they might to some extent be driven by (bio) geography, as some climatic variables were strongly correlated to either latitude or distance from equator. For instance, temperature seasonality increases sharply with distance to equator ($R^2 = .81$), which similarly explains community functional composition (cf. Figure 4 and Supporting Information Figure S7). We can thus only speculate about the relative importance of climatic and geographic gradients, as they share the largest fraction of explained variance in CWM traits. However, we note that both climate and geography have also unique effects on community functional composition (Table 2). To illustrate this, the southern Brazilian Atlantic Forest does not fully follow the trend of increasing dominance of opportunistic strategies with distance from equator, as it supports many large, hard-wooded trees. This can, however, be explained by combinations of climatic factors, given the seasonal but relatively cold and dry climates in the southern (compared to the northern) extreme of the Neotropics (Figure S1), which select for conservative strategies. In fact, most species in this southernmost region have tropical-subtropical ranges due to forest expansion over subtropical grasslands during the Last Glacial Maximum (Costa et al., 2018; Oliveira-Filho et al., 2013). Also, the dominance of species with small leaves and conservative traits under wet and warm climates in the Caribbean region deviates from the trait-climate relationships, but may reflect selection by hurricane-force winds for stronger structural support (Lugo, 2000).

There is a consensus that climate change will make tropical forests warmer, with more seasonal rainfall and temperature including more frequent droughts, more heavy rains and frequent heatwaves (IPCC, 2014). These are conditions currently found across northern Neotropical moist forest regions, where opportunistic

strategies thrive. Therefore, it is reasonable to expect forests in northern Neotropical regions to be more resilient to predicted climate changes, unless climate change leads to drastic changes towards alternative ecosystem states, like dry forest or woodlands. In contrast, climate changes should lead southern and especially equatorial forests of the future to more closely resemble today's northern Neotropical moist forests due to proliferation of opportunistic strategies already present in regional species pools (Figure 2a). This may disrupt ecosystem services such as carbon sequestration and storage if forests once dominated by conservative traits experience the proliferation of more opportunistic strategies (Poorter et al., 2017), including soft-wooded species that grow fast but die young (Brienen et al., 2020).

In summary, tree communities across Neotropical moist forests are functionally distinct because particular traits are favoured under particular climates. Such functional predictability permits insights into tropical forest responses to global changes and the consequences for biodiversity persistence, provision of ecosystem services and global sustainability (Díaz et al., 2007). In fact, as ecosystem functioning is determined by the dominant traits in tropical forests (Poorter et al., 2017), our findings can help to anticipate the impact of future climate change and/or human-induced disturbances (e.g. habitat loss, fragmentation) on the functioning of Neotropical forests. For instance, we must expect an increase in prevalence of low-statured tree species with relatively acquisitive traits and small seeds, based on scenarios of increasing climate seasonality (IPCC, 2014). This functional strategy is associated with faster growth and reproductive rates (Moles, 2018; Reich, 2014) and thrives in human-modified tropical landscapes worldwide (Laurance et al., 2006; Santos et al., 2008), but plays a limited role in crucial ecosystem services such as carbon and nutrient retention (Poorter et al., 2017). Overall, this changing functional structure of Neotropical moist forests is likely to confer varying degrees of resilience to human-caused disturbances. Neotropical moist forests vary widely in functional terms and one should be aware of these differences when it comes to understanding the functional assembly of Neotropical tree communities.

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AUTHOR CONTRIBUTIONS

BXP, MT and FPLM conceived the ideas and designed methodology; BXP collected, compiled and analysed the data, with the supervision of CtB on the dc-CA analysis; BXP wrote the first draft with significant contributions from FPLM. All authors contributed data and/or critical insights that improved the manuscript.

DATA AVAILABILITY STATEMENT

Data and R codes used for the analyses are available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.vq83bk3s3>. The dc-CA variation decomposition with statistical tests of Table 2 is available at <https://doi.org/10.6084/m9.figshare.13259534.v2>.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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