Received: 27 August 2022 | Revised: 16 October 2023 | Accepted: 2 November 2023

DOI: 10.1111/geb.13790

Global Ecology and Biogeography | A Journal of Macroecology

WILEY

RESEARCH ARTICLE

Global patterns and environmental drivers of forest functional composition

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Funding information
Natural Sciences and Engineering Research Council of Canada

Handling Editor: Arndt Hampe

Abstract

Aim: To determine the relationships between the functional trait composition of forest communities and environmental gradients across scales and biomes and the role of species relative abundances in these relationships.

Location: Global.

Time period: Recent.

Major taxa studied: Trees.

Methods: We integrated species abundance records from worldwide forest inventories and associated functional traits (wood density, specific leaf area and seed mass) to obtain a data set of 99,953 to 149,285 plots (depending on the trait) spanning all forested continents. We computed community-weighted and unweighted means of trait values for each plot and related them to three broad environmental gradients and their interactions (energy availability, precipitation and soil properties) at two scales (global and biomes).

Results: Our models explained up to 60% of the variance in trait distribution. At global scale, the energy gradient had the strongest influence on traits. However, within-biome models revealed different relationships among biomes. Notably, the functional composition of tropical forests was more influenced by precipitation and soil properties than energy availability, whereas temperate forests showed the opposite pattern. Depending on the trait studied, response to gradients was more variable and proportionally weaker in boreal forests. Community unweighted means were better predicted than weighted means for almost all models.

Main conclusions: Worldwide, trees require a large amount of energy (following latitude) to produce dense wood and seeds, while leaves with large surface to weight ratios are concentrated in temperate forests. However, patterns of functional composition within-biome differ from global patterns due to biome specificities such as the presence of conifers or unique combinations of climatic and soil properties. We recommend assessing the sensitivity of tree functional traits to environmental changes in their geographic context. Furthermore, at a given site, the distribution of tree functional traits appears to be driven more by species presence than species abundance.

KEYWORDS
biogeography, climate, environmental gradients, functional traits, seed mass, species abundance, specific leaf area, trees, wood density

1 | INTRODUCTION

The global distribution of forest biomes is well explained by few climatic variables (Holdridge, 1947; Suzuki et al., 2006) and transitions from one biome to the next are generally accompanied by an increase in species richness from the poles to the equator (Hillebrand, 2004). However, our understanding of how species differ in terms of adaptive strategies (e.g. survival, reproduction and resource acquisition) and their related functional traits along global abiotic gradients such as climate is still underdeveloped. Due to the importance of forests worldwide in providing essential ecosystem services (Gamfeldt et al., 2013), understanding the mechanisms that underpin forest community function and assemblage along environmental gradients is needed to predict changes in their composition resulting from shifts in climate and land use.

Abiotic gradients should affect the trait composition of forest communities through complex interplays among temperature, precipitation and soil properties (Joswig et al., 2022; Maire et al., 2015; Ordoñez et al., 2009; Simpson et al., 2016). However, many large-scale studies have assessed trait–environment relationships using univariate models (Bruelheide et al., 2018; Moles et al., 2014; Šímová et al., 2015; Swenson et al., 2012; Swenson & Enquist, 2007; Swenson & Weiser, 2010; Wieczynski et al., 2019), thereby assuming that one environmental variable

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act independently from another, and that the environment constrains functional traits similarly everywhere. This could explain why global scale studies have led to mixed results (Moles, 2017) or broad conclusions that do not capture the unique combined effects of precipitation, temperature and soil properties occurring within-biomes (Wigley et al., 2016).

The relative importance of environmental gradients on forest functional composition should differ among biomes. For instance, we would expect a higher influence of temperature on traits in boreal forests, where the average temperature is low and highly seasonal, compared to tropical forests, where temperatures are warm year-round. In contrast, precipitation can be more limiting in tropical forests, which are subject to both the highest annual precipitation and precipitation seasonality on Earth. Energy availability could drive trait values in temperate forests due to the large range of temperature and solar radiation in this biome, and a weaker effect of precipitation and soils that are generally less variable and fertile respectively. While these are merely simplifications of biome specificities, including interactions among abiotic variables in models and comparative analysis at different scales (global vs. biomes) should account for the contrasting effects of environmental gradients among and within biomes. These additions would provide a more comprehensive understanding of the global functional biogeography of trees beyond generalizations (e.g. latitudinal gradient, dominant effect of temperature) that do not necessarily capture variation at finer scales such as biomes and communities.

Trait–environment relationships are generally stronger when constituent species abundance is included (Ackerly et al., 2002; Cingolani et al., 2007; Fortunel et al., 2014), although the opposite has been observed (Bjorkman et al., 2018; Dubuis et al., 2013; Pakeman et al., 2008). Indeed, based on the mass ratio hypothesis, relative abundance is a good proxy of plant fitness since dominant species are assumed to be the most adapted to an environment (Grime, 1998; Shipley et al., 2011). Yet, the availability of data especially at global scale can be a limitation to including species abundances in analyses of tree trait–environment relationships (Keppel et al., 2021). Many studies that focused on trait–environment relationships at large spatial scales have relied on presence–absence data aggregated to a coarse spatial grain (Chave et al., 2009; Joswig et al., 2022; Maire et al., 2015; Moles et al., 2014; Ordoñez et al., 2009; Šímová et al., 2015; Swenson et al., 2012). The presence–absence data employed in these studies provide no information on relative abundances of species in local communities. Therefore, the mass ratio hypothesis remains to be tested globally.

Recent studies on the global distribution of plant functional traits tend to include a large number of functional traits (Joswig et al., 2022; Maynard et al., 2022) and moments (Wieczynski et al., 2019). This high level of information precludes describing thoroughly each individual trait–environment relationship. Moreover, the lack of data for most of these traits limits our ability to study their global distribution at community levels. Here we focus on three key functional traits for which we aim to provide the most comprehensive explanation and visualization of their composition within global forest communities, while accounting for the simultaneous and interacting effects of environmental gradients. We describe, illustrate, and compare each trait–environment relationship, its effects, magnitude and importance across scales and biomes.

The selected traits are wood density (WD), seed mass (SM) and specific leaf area (SLA) because they are commonly measured and offer broad data coverage. They emerge strongly as predictors of different life history strategies (Chave et al., 2009; Westoby, 1998) and important axes of global plant form and function (Díaz et al., 2016). These functional traits can be used to reflect a gradient of acquisitive to conservative strategies among species. Resource conservative species tend to have higher WD and SM, lower SLA and are characterized by larger construction cost, greater longevity, but lower productivity of plant organs, relative to faster-growing acquisitive species. We explore separate and joint effects as well as the importance of trait–environment relationships using both weighted and unweighted trait means of forest communities across three abiotic gradients: energy availability (temperature and solar radiation), precipitation and soil properties, at biome (boreal, temperate and tropical) and global scales. To this end, we use an unprecedented data coverage that includes tree species abundance from between 99,953 and 149,285 sample plots, depending on trait.

We address three specific questions: (1) How is the functional trait composition of forest communities constrained by abiotic environmental gradients worldwide? We expect energy, precipitation and soil properties to influence functional trait values conjointly, including contrasting patterns among and within biomes that would be revealed through interactions between and within these environmental gradients. (2) How important are environmental gradients and their interactions in explaining the distribution of functional traits of forest communities? We expect that, at global scale, energy availability would be the most important gradient in explaining trait distribution due to the significant changes of this gradient along latitude; but gradient importance within-biome models could differ substantially from global models. (3) Does accounting for species abundance strengthen these trait–environment relationships? Based on the mass ratio hypothesis, we would expect weighted trait values to be better predicted than unweighted values.

2 | METHODS

2.1 | Forest inventories

Our ground-sourced forest inventory data were compiled by the Global Forest Biodiversity Initiative (GFBI) from approximately 1.2 million sample plots in more than 70 countries (see Liang et al., 2022 for methodology, and data & code availability). Individual tree data consisted of standard tree-level measurements of 54,864,083 individual trees in 29,691 species and morpho-species. A worldwide species abundance matrix was produced from individual tree data. Species in this matrix were joined with functional traits using their taxonomic name (see Appendix S1 in Supporting information for taxonomic cleaning procedure). For plots with multiple measurements

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over time, only the most recent measurement was used in the analysis. Tree ferns and bamboos were removed from the analyses.

2.2 | Functional traits

Functional trait values were extracted from the TRY database (Kattge et al., 2020) and completed via a literature review (Appendix 1). We cleaned data from all sources to remove duplicates, values beyond reported ranges (Pérez-Harguindeguy et al., 2016), and measurements from seedlings in greenhouses and experiments evaluating stress response (Appendix S1). Depending on the functional trait, the total number of documented species varied between 3923 and 7252 (Table 1). A mean per species per trait was computed and attributed to the individuals of this species in the forest inventories. Then, community-weighted means (CWM) of traits in each plot were calculated using the number of stems per species as the weight. Community unweighted means (CM) were computed by giving the same weight to each species in the plot. We included only those plots with a minimum of 80% of constituent species with trait information based on the number of stems following other studies (Garnier et al., 2004; Grime, 1998; Pakeman & Quested, 2007). In the final analysis, we retained between 99,953 and 149,285 plots, which covered all of Earth's major biomes (Table 1, Figure 1, Appendix S2).

2.3 | Climatic and pedologic variables

Precipitation-, temperature- and solar radiation-related variables were obtained through the WorldClim database as 30-year averages (1970 to 2000) at a resolution of 30 arcseconds (~1 km^2 at the equator) (Fick & Hijmans, 2017). We compiled seven soil variables from the SoilGrids database for a depth of 0 to 30 cm at a resolution of 250 m (Hengl et al., 2017). These variables were selected to represent three broad environmental gradients: energy availability (including temperature and solar radiation), precipitation and soil properties (Table 2). Climatic and pedologic values were extracted using plot spatial coordinates.

2.4 | Data analysis

We conducted multiple linear regressions with second-order polynomials to account for the polynomial or linear relationships observed in raw data between traits and environmental variables. We built four models per trait with data fitted at different scales and biomes: global forests (all data), boreal forests, temperate forests and tropical forests. Biome-related results were obtained using biome-level models trained on data coming solely from the studied biome. Global patterns were assessed using the full dataset. Biomes were based on the World Wildlife Fund classification (Olson et al., 2001). Subtropical forests were grouped with tropical forests, whereas temperate forests of broad-leaves and/or conifers were included in the temperate biome along with Mediterranean forests. The complete list of terrestrial ecoregions included in larger biomes (boreal, temperate and tropical) is available in Appendix S3. All analyses were conducted in R statistical software, version 4.1.0 (R Core Team, 2020).

To control for multicollinearity, we conducted variable selection based on standardized generalized variance inflation factors (GVIF) implemented in the '*car*' package (Fox & Weisberg, 2019). Predictors were removed until no more variables would exceed a threshold of GVIF = 2 in the model, which is equivalent to a variance inflation factor (VIF) threshold of 4. When selecting variables, we prioritized keeping at least two variables per gradient, since we were interested in the combined effects of all gradients. Seed mass was transformed by a natural logarithm because this trait is inherently multiplicative and spans orders of magnitude (Kerkhoff & Enquist, 2009). All assumptions related to regression models were respected (normality, homogeneity of variance, linearity and independence) except for normality in seed mass models. Therefore, seed mass models were bootstrapped using 10,000 iterations to compute confidence intervals (percentile) to ensure that deviations from normality would not underestimate error terms. We tested two-way interactions within gradients (three intra-gradient interactions) and two-way interactions between gradients (three inter-gradient interactions) (Appendix S4 for more details on data analysis).

Initial variable selection was performed for each trait at both global and biome scales. In some cases, models could differ in the inclusion of specific variables within each gradient. To ease interpretation and comparability between models, we also examined models using identical variables between global and biome scale models (although polynomials could differ). We found similar predictions of community means for each trait between the biome- and global-scale models (Appendix S5). For ease of interpretation, here we opted to display the models that include the same variables. All selected variables and interactions appear at the left of the panels in Figure 3. Variable importance was assessed using dominance analysis with the '*dominanceanalysis*' package (Bustos Navarrete & Coutinho Soares, 2020). To ensure that the uneven plot

TABLE 1 Documented species per trait and number of plots per trait and biome.

	Taxonomy				Number of plots			
Functional traits	Species	Angiosperm	Gymnosperm	Families	Global	Boreal	Temperate	Tropical
Wood density	7252	7045	213	194	149,285	8783	138,081	2393
Specific leaf area	4930	4794	136	205	131,979	4870	125,677	1416
Seed mass	3923	3687	239	203	99,953	4831	94,058	1050

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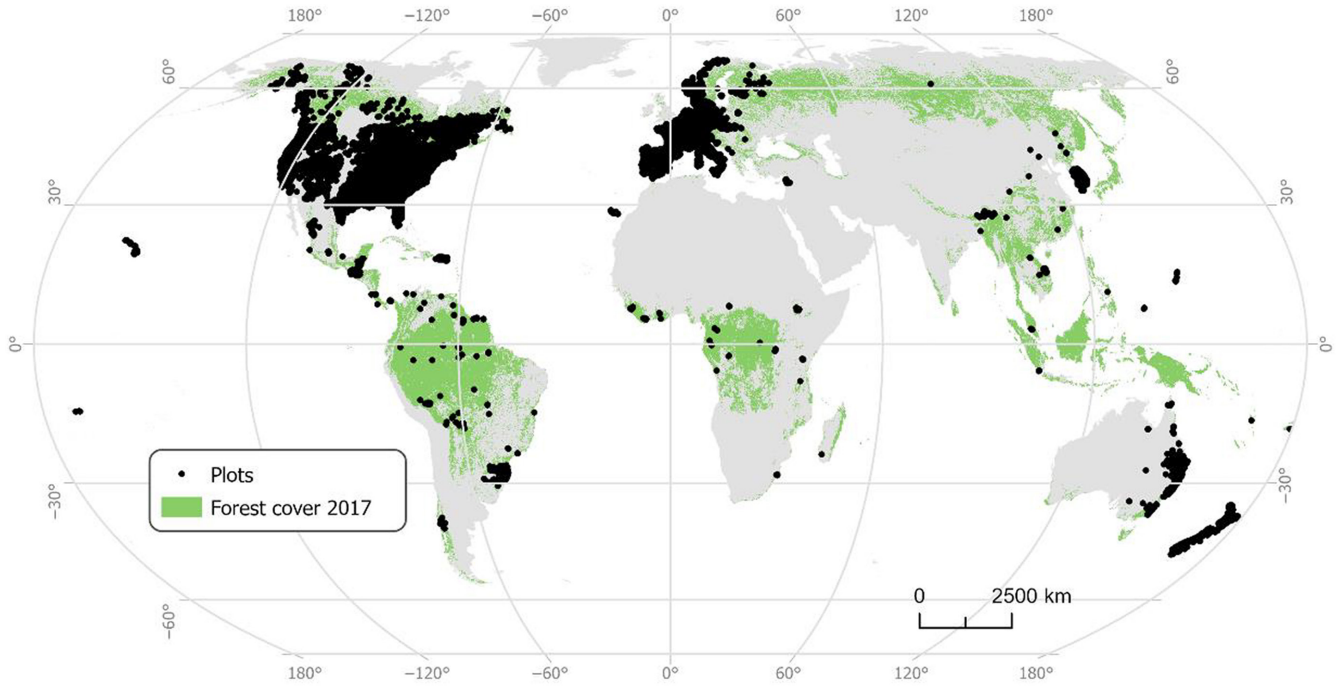

FIGURE 1 Geographical distribution of plots for wood density (total number of plots: 149,285), specific leaf area (total number of plots: 131,979) and seed mass (total number of plots: 99,953). While most of the plots illustrated on this map are used for all three functional traits, there are small differences in single-trait distributions due to the requirement that trait values needed to be available for 80% of the stems in a plot (see methods). Specific trait distribution maps are available in Appendix S2. Map projection = WGS 1984 Equal Earth (world).

TABLE 2 Variables names, abbreviations, units, ranges and means.

Variable	Abbreviation	Units	Range	Mean
Functional traits				
Wood density	WD	mg/mm^3	0.15 to 1.24	0.55
Specific leaf area	SLA	m^2/kg	1.3 to 169.8	16.4
Seed mass	SM	mg	0.01 to 576,800	860
Environmental variables				
Energy gradient				
Mean annual temperature	MAT	°C	−7.7 to 27.8	12.2
Temperature seasonality	TS	°C *100	27 to 1734	842
Annual mean solar radiation	SR	kJ/m^2*day	7296 to 21,786	14,369
Precipitation gradient				
Annual precipitation	AP	mm	68 to 4712	1175
Precipitation seasonality	PS		5.5 to 120.2	26
Soil properties gradient				
Percentage in clay	CLAY	%	0 to 58.3	18
Percentage in sand	SAND	%	0 to 96.4	43.6
Available water storage capacity	AWC	v%	5.8 to 51.4	44.5
Cation exchange capacity	CEC	cmol+/kg	1.75 to 192.92	19.12
Percentage of organic carbon	OC	‰ (g/kg)	4.2 to 372.6	40.8
pH measured in a soil–water solution	pH	pH*10	37 to 81	53
Bulk density	BULK	kg/m^3	606.5 to 1696.2	1320.4

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distribution would not compromise the regression slopes, we tested the models for spatial autocorrelation among residuals using variograms built with the *'gstat'* package (Pebesma, 2004; Pebesma & Heuvelink, 2016) and k-fold cross validation (Ploton et al., 2020) using the*'blockCV'* package in R (Valavi et al., 2019). The resulting figures showed no pattern of spatial autocorrelation across all models (Appendices S6 and S7). We ran selected models using weighted or unweighted community means as response variable. To determine the effect of abundance weighting on the strength of the relationships between forest communities' mean traits and environmental gradients, we compared model fits using adjusted R^2 and normalized root mean square error (nRMSE). We refrained from presenting any inferential statistics in the main text due to the high level of observations resulting in most coefficients being significant. Instead, we interpret results based on effect size and variance partitioning. However, regression coefficients and associated errors are presented in Appendix S4 for all models.

Finally, we built estimated biogeographic distribution maps of each trait to illustrate global scale patterns along with their associated uncertainty maps (Appendix S8). We derived estimates of global climate and soil properties from the same databases as our training data (WorldClim and SoilGrids) in forested areas identified through the Global Forest Change database (Hansen et al., 2013) since our training dataset was limited to forests. We then used biome-scale models to estimate the trait values for each grid cell, because they feature more detailed changes within biomes than maps fitted using global models. Grid cells that had climate and soil properties values outside the range of our observed values were omitted from mapping.

3 | RESULTS

3.1 | Species abundance

Eleven of twelve models performed better with community unweighted means than with community-weighted means based on nRMSE (Appendix S9) and adjusted R^2. The absolute increases in explained variance for the global models were 11%, 10% and 3% for WD, SLA and SM respectively. Further analyses were conducted using community unweighted means.

3.2 | Effect of environmental gradients on traits

For all trait values, boreal forests had the lowest medians and narrowest ranges (Figure 2). Trait expression varied more in tropical and temperate forests, with higher medians of WD in tropical forests and higher medians of SM and SLA in temperate forests. At global scale, SM showed the strongest relationships with environmental gradients (adjusted $R^2 = 60\%$), followed by WD (adjusted $R^2 = 46\%$) and SLA (adjusted $R^2 = 45\%$). The explained variance of the biome models was 24% (WD), 26% (SLA) and 31% (SM) in boreal forests; 38% (WD), 45% (SLA) and 46% (SM) in temperate forests; and 38% (WD), 49% (SLA) and 26% (SM) in tropical forests (Figure 3).

We produced global prediction maps fitted with our biome-level models to simultaneously visualize the effect of all variables and their interactions (Figure 4). These maps revealed that SLA is the only trait reaching the most acquisitive strategies (high values, that is, leaves with large surface to weight ratios) in temperate forests (Figure 4). In contrast, both WD and SM generally followed a latitudinal gradient from acquisitive strategies (light wood and seeds) in boreal forests to conservative strategies (dense wood and heavy seeds) in tropical forests.

The effect of mean annual temperature on SM and WD was generally positive or unimodal, increasing to an optimum and decreasing thereafter. An exception in tropical forests is that SM decreased slightly along mean annual temperature. Relationships between SLA and solar radiation varied across biomes (Figure 5). Effects of temperature seasonality on traits depended on the biome (Figure 5). Higher temperature seasonality favoured conservative strategies in some instances (SLA in tropical forests and SM in temperate forests) or acquisitive strategies in others (WD and SM in boreal forests, WD in tropical forests and SLA in temperate forests). More nuanced responses by traits to increasing temperature seasonality occurred, with a unimodal response including either an optimum or a minimum (SM in tropical forests, WD in temperate forests) or no clear association (SLA in boreal forests).

Higher annual precipitation favoured conservative strategies of SM in boreal and tropical forests but did not affect temperate forests (Figure 5). Responses of WD to annual precipitation were variable across biomes (Figure 5). As precipitation increased, SLA increased in temperate forests but decreased slightly or remained stable in tropical and boreal forests. The lack of response from SM to precipitation seasonality was consistent across biomes, whereas WD and SLA generally decreased with precipitation seasonality.

The effect of soil properties on SLA was very consistent: soils with more favourable structures (low sand content and high bulk density) favoured acquisitive strategies. Results for SM were also consistent and indicated weak effect of cation exchange capacity (CEC) and soil pH. Wood density was slightly influenced by sand content across biomes. However, higher WD may be favoured by increasing CEC in tropical forests relative to temperate forests, whereas CEC had no notable effect in boreal forests (Figure 5).

These direct effects were modulated by interactions. The high number of variables and interactions prevented us from presenting all direct and interacting effects (but see appendices S10-S12). We selected the most notable ones to display in Figures 5 and 6.

3.3 | Importance of environmental gradients on traits

Globally, the energy gradient dominated the explained variance for WD and SM, with precipitation explaining the smallest amount of variance. Specific leaf area was more evenly influenced by the three gradients, although the energy gradient still explained most of the variance (Figure 2). Interactions between and among gradients strongly influenced trait distributions: the cumulative

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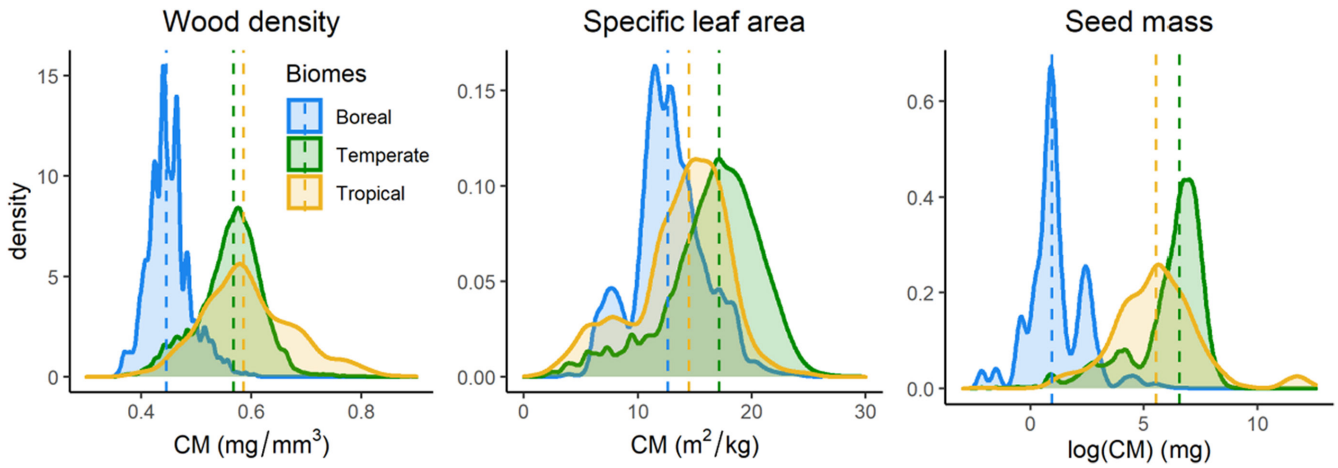

FIGURE 2 Density plots of community unweighted means (CM) per trait and biome. The dashed lines display the median of the distribution.

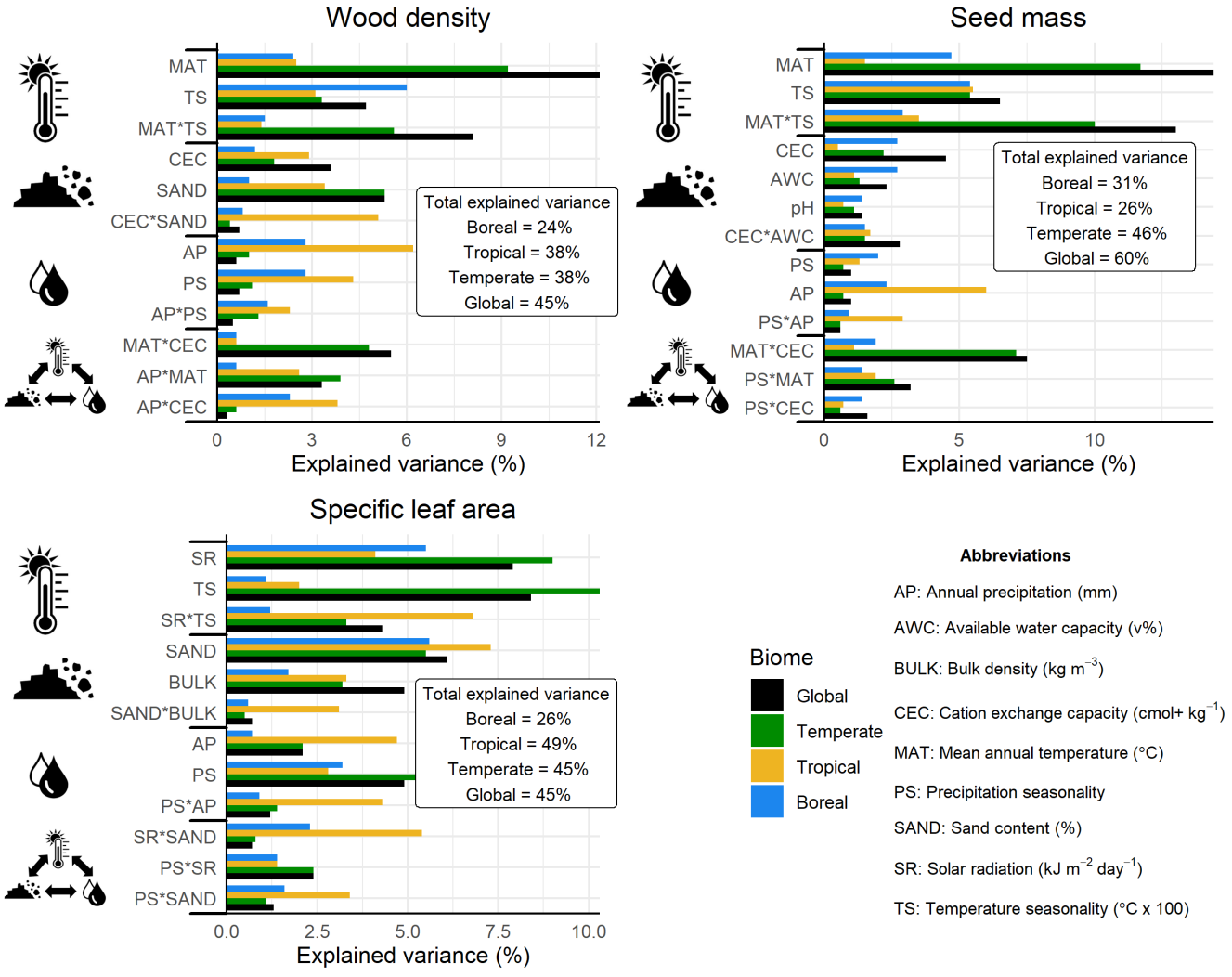

FIGURE 3 Results of variance partitioning from dominance analysis. Bar colours represent different models (boreal, tropical, temperate, global), whereas pictograms on the y axis emphasize the gradient to which the variables belong (energy availability, soil properties, precipitation or an interaction between gradients). Interactions are symbolized by an asterisk * between the variable abbreviations. The total explained variance of a model (adjusted R^2) is displayed in the label box and equals the cumulative weight of all bars from a same model.

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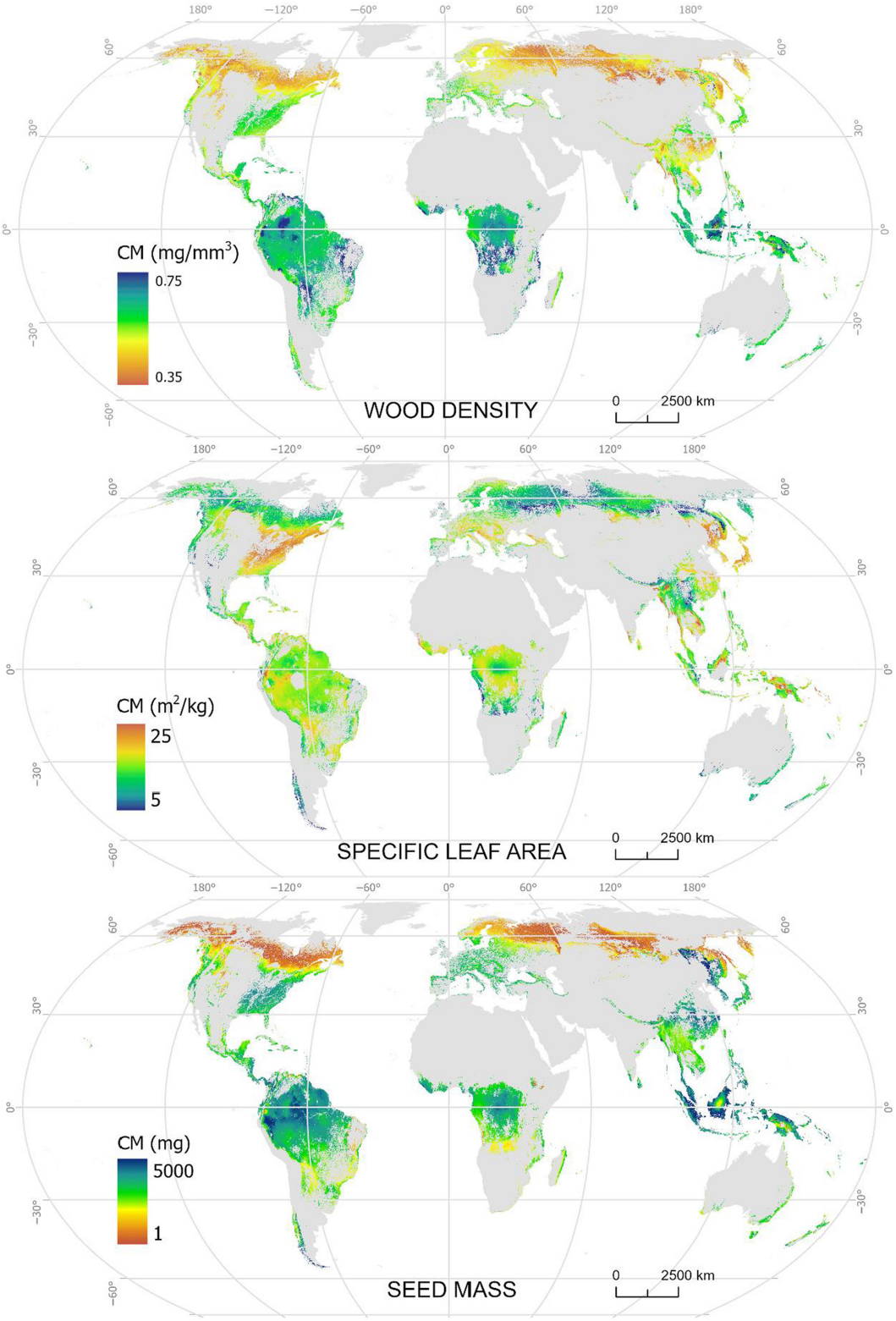

FIGURE 4 Biogeographical representations of the explained distribution of functional traits of trees. The colour palette represents a gradient from acquisitive strategies (red-yellow) to conservative strategies (green-blue). Map projection, WGS 1984 Equal Earth (world).

explained variance due to interactions in global-scale models were 18% (WD), 11% (SLA) and 29% (SM). Within biomes, the cumulative explained variance due to interactions were 7% (WD), 8% (SLA) and 10% (SM) in boreal forests; 17% (WD), 10% (SLA) and 22% (SM) in temperate forests; and 16% (WD), 24% (SLA) and 12% (SM) in tropical forests.

Boreal forest functional trait responses varied under the influence of environmental gradients. Wood density was best predicted

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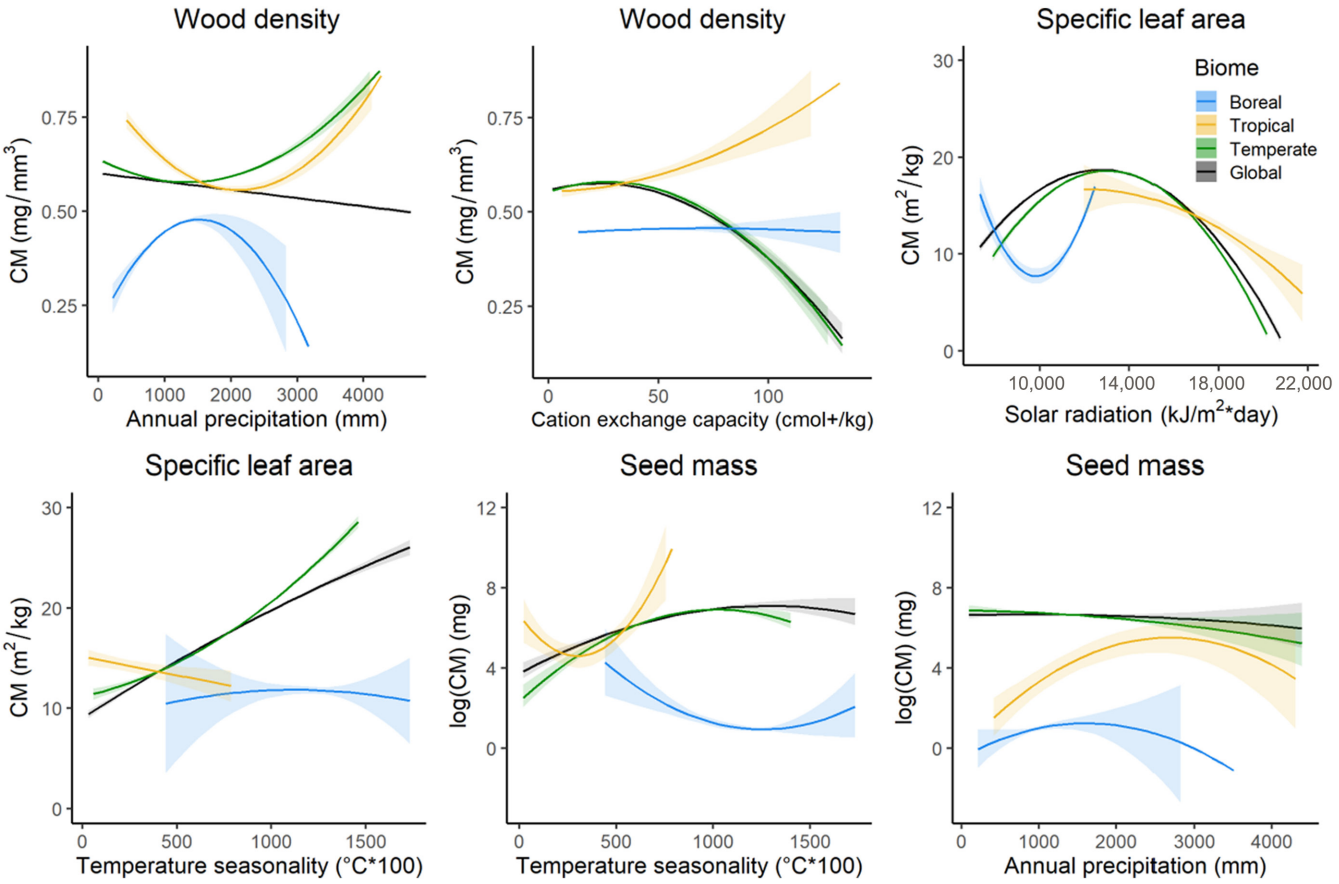

FIGURE 5 Effect plots of environmental variables on community unweighted means (CM) of traits. Lines and colours represent different scales and biomes. Bands around lines represent 95% confidence intervals.

by energy and precipitation with less influence from soils. Seed mass was also primarily influenced by energy, followed by soil properties and precipitation. For SLA, soil properties dominated the explained variance along with energy, while precipitation had less influence. For temperate forests, energy had a dominant effect on all traits with precipitation having the least influence (WD and SM) or affected equally by soils and precipitation (SLA). In tropical forests, WD was best explained by precipitation and soil properties with energy the least important gradient. Specific leaf area was strongly influenced by soils and energy, with precipitation still explaining much of the variance. Seed mass was almost equally influenced by energy and precipitation with less influence from soil properties.

4 | DISCUSSION

4.1 | Global patterns

On a global scale, the studied functional traits responded strongly to macroenvironmental gradients, with about half the variance among traits explained. This strong signal demonstrates that local communities of tree species respond to large-scale fluctuations in climate and soil properties, contradicting results from Bruelheide et al. (2018) who studied univariate trait–environment relationships in vegetation plots at large scale. This difference may arise from the inclusion of simultaneous effects of multiple environmental variables in our study since environmental variables act jointly in filtering tree strategies. Also, trees as long-lived organisms may be more responsive to macro environmental gradients compared to other plant life forms. Plants with shorter life spans operate at smaller temporal scales and could be more sensitive to local climate and biotic conditions (Levin, 1992).

Our prediction maps revealed that WD and SM generally followed a latitudinal gradient, whereas SLA did not, although we did not test directly for latitude but rather for associated variables (energy availability). Traits related to organ size are believed to respond to latitude due to their dependence on available energy (Joswig et al., 2022; Moles et al., 2006), which was validated for SM in our study. On the other hand, SLA is considered an economic trait and should respond mostly to latitude-independent soil and climate variables (Joswig et al., 2022), which is consistent with our results. Wood density is considered an intermediate trait (Díaz et al., 2016; Joswig et al., 2022) that clusters more closely with economic traits (Joswig et al., 2022). However, WD displayed a latitudinal gradient in our prediction maps, indicating that trees rely on available energy to produce dense wood, even though this trait is not directly linked to tree size but mostly to plant performance (Chave et al., 2009).

Globally, the effects of energy availability on traits distribution were unimodal, suggesting the existence of optimums for tree organ

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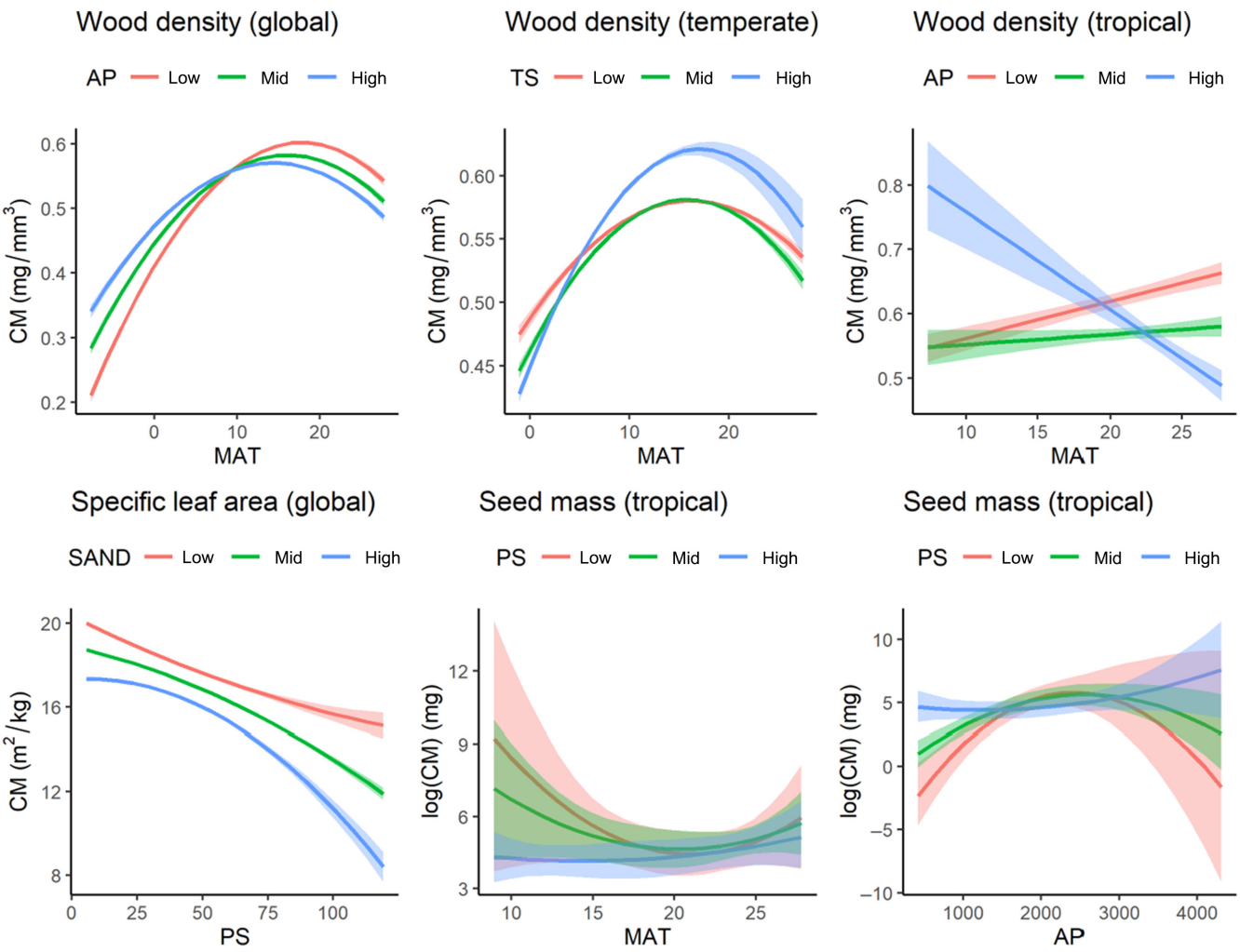

FIGURE 6 Predicted graphs of interactions among climatic and soil variables in relation to community unweighted mean (CM) of traits for different scales or biomes. Bands around lines represent 95% confidence intervals. The categories of explanatory variables (low, mid, high) denote the 10th, 50th and 90th percentile of their distribution. AP, annual precipitation (mm); MAT, mean annual temperature (°C); PS, precipitation seasonality; SAND, sand content (%); TS, temperature seasonality (°C*100).

functioning. Specific leaf area reached the most acquisitive strategies at intermediate values of solar radiation (around 13,000 kJ m^{-2} day^{-1}). Conservative strategies of WD and SM reached an optimum at mean annual temperatures around 15°C, consistent with results of Maynard et al. (2022). However, tropical forests did exhibit the highest values of WD and SM. The decline observed after these temperature optimums seems to reflect a transition away from energy to other limiting factors in tropical forests (soils properties and precipitation) rather than a theoretical optimum of temperature after which traits values are constrained by further increases in energy availability.

Energy availability had the strongest influence on functional traits on a global scale. Indeed, mean annual temperature and solar radiation are the variables that best align with latitude. Precipitation and soil properties show greater heterogeneity along latitudes compared to energy, so it is plausible that their effect is more easily detectable at biome scales, as reflected in our data. This might explain why precipitation and soil effects on traits distribution are seldom strongly detected at global scale compared to temperature patterns (De Frenne et al., 2013; Maire et al., 2015; Maynard et al., 2022; Moles et al., 2014; Wieczynski et al., 2019). In sum, few trait–environment relationships were consistent across scales and biomes, confirming the necessity to investigate the biogeography of traits at the biome level.

4.2 | Effects of environmental gradients on forest functional composition

4.2.1 | Wood density

Wood density is an important component of tree longevity, mechanical strength, hydraulic safety, and growth rate (Chave et al., 2009). The lowest median and narrowest range of WD were found in boreal forests, reflecting the dominance of conifers. Their wood is mostly composed of tracheids, which allows a greater resistance to frost-induced cavitation than the vessels of broad-leaf species at

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similar WD (Hacke et al., 2001). Temperature seasonality was the most limiting factor in the boreal biome: shorter growing seasons came with lower wood densities. In contrast, we observed a decline in the importance of temperature seasonality relative to mean annual temperature in temperate forests compared to boreal forests, possibly reflecting a threshold in the influence of seasonality on broad leaf species presence. Broad leaf species may out-compete conifers where there are fewer than about two months of frost per year (Crawford, 1989) leading to higher community WD. Temperate species invest more in their wood as mean annual temperature increases. However, this positive relationship between WD and temperature reached an optimum, and subsequent increases in mean annual temperature in tropical forests had much less impact than in other biomes relative to soil properties and precipitation gradients. In the tropical biome, temperature seasonality became slightly more important than mean temperatures again, with lower wood density values towards subtropical forests, as also observed by Pinho et al. (2021).

Worldwide, sand content impacted consistently wood density in forest communities, with a small shift of similar magnitude (±0.01 mg/mm3 per 20% change in sand content). In the northern biomes (boreal and temperate forests), trees tended to develop denser woods on finer soil texture (lower sand content). Many areas of these forests, characterized by coarser soils, host coniferous species (mostly pines) explaining the trend towards lighter woods. On the contrary, WD slightly increased with sand content in tropical forests, confirming patterns observed in Amazonia (Fortunel et al., 2014; Ter Steege et al., 2006; Vleminckx et al., 2021) and African tropical forests (Réjou-Méchain et al., 2021) where broadleaf species tend to adopt conservative resource-use strategies in poorer soil habitats. In addition to soil texture, cation exchange capacity was highly influential in explaining variation of WD in tropical forests, independently and in interaction with sand content and annual precipitation. Tropical forests are characterized by infertile and acidic soils (Kricher, 2017) explaining why soil properties might be more of a constraint towards conservative strategies in this biome.

We found that the precipitation gradient had minimal effect on WD at global scale, as also reported by others (Costa-Saura et al., 2016; de la Riva et al., 2018; Šímová et al., 2015; Wiemann & Williamson, 2002; Zhang et al., 2013). Despite the main effects being unimportant, the interaction between precipitation and temperature was notable. Higher WD was associated with more arid environments as expected because of greater resistance to drought-induced cavitation associated with high WD in broad-leaf species (Greenwood et al., 2017; O'Brien et al., 2017). Precipitation was the most influential gradient driving the distribution of WD in tropical forests. Wood was denser at higher temperatures when annual precipitation was low, which can indicate an arid climate. However, WD seemed to be higher in tropical forests that are either drier or wetter throughout the year, than in habitats that are periodically arid with high seasonal changes in precipitation regimes. This effect may be due to other protection mechanisms to drought cavitation in seasonal tropical forests, such as leaf shedding during the dry season. These interactions between annual means and seasonality could explain the mixed results reported in the literature, with reports of higher values of WD in areas with high rainfall (Ordoñez et al., 2009; Swenson et al., 2012; Swenson & Weiser, 2010; Zhang et al., 2011), in arid environments (Cornwell & Ackerly, 2009; Preston et al., 2006; Swenson & Enquist, 2007) or at average precipitation regimes (Wiemann & Williamson, 2002). In boreal forests, higher precipitation allowed for more conservative strategies, which may be associated with a lower risk of forest fires. This reduced risk of fire gives more opportunity for establishment of late successional species which typically have high WD.

The WD of trees was associated with survival strategies that are increasingly conservative and diversified as we moved from boreal to tropical forests (Stahl et al., 2014), probably due to fewer constraints from temperature and its seasonality, and increasing biotic pressure leading to more divergent strategies (Swenson & Enquist, 2007; Terborgh, 1973) and higher constraints on wood mechanical strength (Kricher, 2017). Regardless of biome or scale, our results were consistent with the role of WD related to hydraulic safety in trees (Chave et al., 2009; Swenson & Enquist, 2007). Lower values were found where the growing season is short and temperature is low (the presence of conifers and frost-cavitation avoidance), and higher values where the climate is drier (drought cavitation avoidance).

4.2.2 | Specific leaf area

Specific leaf area is the amount of biomass invested in building a given light-intercepting leaf area (Wright et al., 2004). Our results for SLA are consistent with a dominant role of resource investment in governing this trait, since we observed a more balanced importance of environmental gradients linked to resources availability (light, precipitation and soil properties) than in the other functional traits. Specific leaf area is the only trait for which solar radiation was selected over mean annual temperature, confirming the strong links between light availability and this functional trait (Wilson et al., 1999). Specific leaf area is expected to decrease with higher irradiance following a non-linear relationship (Poorter et al., 2009). Instead, our large-scale analysis showed a unimodal relationship with an optimum (acquisitive strategies) found at average solar radiation in temperate forests. This is likely due to light-independent stresses that limit leaf productivity in other biomes. Evergreen species are known to have lower SLA in trees than deciduous species (Villar & Merino, 2001). Indeed, trees in both boreal and tropical forests likely invest more heavily in their leaves than their temperate counterparts since they both include evergreen species with leaves highly adapted to survive winter (boreal forests) or are subjected to herbivory that require higher levels of investment in defence (tropical forests; Sedio et al., 2018). On the other hand, in many areas temperate forests are characterized by seasonal leaf shedding, which is highly influential in the dynamics of leaf development and longevity. The acquisitive strategies

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of leaves observed in this biome are likely adapted to their short residence time, which is confirmed by a pronounced importance of temperature seasonality over solar radiation in temperate forests relative to boreal and tropical forests.

Specific leaf area increased (acquisitive strategies) with annual precipitation and decreased with precipitation seasonality, which tends to confirm the conservative strategies of this trait reported for xeric environments (Cornwell & Ackerly, 2009; Costa-Saura et al., 2016; Wright et al., 2005) as an adaptation to withstand drought (Greenwood et al., 2017; O'Brien et al., 2017). The negative effect of precipitation seasonality was generalized across biomes, whereas annual precipitation had smaller effects on SLA in tropical and boreal forests than in temperate and global forests, providing further evidence that these biomes are possibly constrained by freezing and herbivore defence respectively.

Specific leaf area tended to exhibit more acquisitive strategies on soil with a favourable structure (i.e. higher bulk densities and lower sand content), especially when precipitation inputs were stable throughout the year. This trend is consistent across the three biomes, but most prominent in tropical forests where soil variables explained more variance in SLA than energy variables. This finding is consistent with the hypothesis that SLA responds strongly to soil variables when soil fertility is low, such as in tropical rainforests (Fortunel et al., 2014; Vleminckx et al., 2021; Wright et al., 2004).

Surprisingly, almost all models of SLA had high predictive power (45% to 49% R^2_{adj}) and large effect size, with the possible exception of boreal forests (26% R^2_{adj}). Typically, evidence of relationships between SLA and abiotic factors such as soil fertility, temperature and precipitation is extremely weak or inconsistent across studies (Moles, 2017). It is possible that SLA responds more strongly in trees than in other plant life forms; thus, when all plants are pooled, the signal may be weaker or lost as previously observed (Bruelheide et al., 2018; Gong & Gao, 2019). Our results validated that in stressful environments where plant growth is limited whether by cold, drought or soil properties, tree species tend to invest in tougher, longer lived leaves, maximizing reserves rather than resource acquisition, at the expense of growth (Grime, 1977; Poorter et al., 2009).

4.2.3 | Seed mass

Seed mass is related to the reproductive effort in plants, through its negative relationships with seed production, dormancy, persistence in the soil and positive relationships with seedling size and survival (Moles, 2017). It has been suggested that temperature and precipitation may be important drivers of the latitudinal gradient in SM (Lord et al., 1997). At global scale, we observed a strong effect of both mean temperature and its seasonality on SM, but very little effect of precipitation. Others have also associated this latitudinal gradient with broad vegetation types (Moles et al., 2007). The lightest seeds were indeed found in boreal forests with a low range of values and the dominance of wind dispersal strategies. The heaviest seeds occurred in tropical forests, as previously observed (Lord et al., 1997; Moles et al., 2007), with community means fifteen times heavier than in temperate forests, but interestingly the median was lower due to the broad range of seed strategies (e.g. wind vs. animal dispersal) encountered in this biome (Malhado et al., 2015).

Seed mass was the most consistent trait across scale and biomes and responded best to the energy gradient. The literature attributing heavier seeds to the warmest temperatures is vast (Malhado et al., 2015; Moles et al., 2014; Šímová et al., 2015; Simpson et al., 2016; Swenson et al., 2012; Swenson & Weiser, 2010; Wieczynski et al., 2019). Our global and temperate models validated a positive relationship of SM with mean annual temperature but only to a certain point, after which it declined. This decrease at very warm temperatures seems surprising, but analysis in tropical forests showed that the direction of this relationship in this biome depends on precipitation regimes and mean annual temperature alone explained little of the variance relative to temperature seasonality. In fact, at both temperature extremes (cold in boreal forest and warm in tropical forests), the variation of temperature across seasons was more limiting on reproduction strategies than mean annual temperature alone. Trees tended to invest in heavier seeds in boreal forests if temperature across seasons was more even, probably due to more energy available to invest in reproduction with longer growing seasons. Whereas in tropical forests, the impact of mean annual temperature was pronounced only if it fluctuated significantly over the year (as in subtropical forests). Seeds were generally heavier in these seasonal forests, possibly because there are less diverse strategies than in warmer tropical forests, and their mass decreased along mean annual temperature up to 17°C. In warmer tropical zones (>18°C of mean annual temperature), SM increased slightly with temperature.

The importance and the effect of soil pH were minimal, indicating that throughout the world similar values of seed masses are found under different pH values, as previously observed in temperate forests (Simpson et al., 2016). Selected soil variables had weak importance, or minimal effects in all biomes. In light of these results, it is challenging to identify trends in the effect of soil properties on SM, confirming the mixed results (Moles, 2017) or the complex interplays between soil fertility and this trait (Simpson et al., 2016) reported in literature.

The global effect of precipitation on SM was weak, which contradicts results of studies at broad geographic scales in which precipitation was tested against traits alone, without the possible interactions with other drivers (Moles et al., 2014; Swenson et al., 2012; Swenson & Weiser, 2010). Nevertheless, models fitted at biome scale revealed that in boreal and tropical forests the effect of annual precipitation on SM was positive. Tropical forests contrasted with other biomes by being strongly influenced by precipitation regimes. Seed mass increased with annual precipitation and this relationship was modulated by precipitation seasonality. When annual precipitation was low, the presence of a dry season favoured higher seed mass, probably because many trees in seasonal tropical forests drop their seeds at the onset of the rainy season. Therefore, the seeds are not subject to as much water stress as those in tropical forests that are drier year-round. The hypothesis of higher seed mass in arid environments

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(Baker, 1972; Pakeman et al., 2008) was not supported by our data at any level. Low water input seems to limit conservative strategies of SM in trees. We would expect tree species to exhibit lower SM when subjected to harsh environmental conditions, because plants growing in stressful conditions tend to assign a lower proportion of annual carbon to reproduction (Grime, 1977). Our results validated this trend for energy and water limitations, but not for soil fertility.

4.3 | Importance of environmental gradients on forest functional composition

In boreal forests, energy availability was influential for all traits but sometimes was equal to soil properties (SLA) or followed closely by precipitation (WD). Therefore, the dominant effect of temperature was not as pronounced as expected. Some traits may be more influenced by environmental conditions that act during the growing season (precipitation and soils), rather than the dormant season (cold temperature). In summary, strategies of boreal trees did not respond as strongly as those in the other biomes to shifts in environmental gradients, suggesting that they might be proportionally less affected by changes along these gradients. On the other hand, a limited range of trait values may restrict their ability to cope with these changes. The trait composition of boreal forest communities could also be constrained by a disturbance gradient, such as large-scale insect epidemics (Gauthier et al., 2015) that was not considered in this study, relative to temperate and tropical forests that are both characterized by smaller scale disturbance patterns.

Trait variation in temperate forests was generally well explained by environmental gradients. Functional traits are known to differ greatly between broadleaves and conifers (Stahl et al., 2013). The alternation of pure or mixed coniferous and broad-leaf forests found in this biome may explain this result through substantial transitions in functional traits values. Temperate forests were the only biome for which a single gradient emerged as the most important across traits. We observed the expected strong influence of energy availability due to the large range of temperature and solar radiation encountered along with a weaker effect of precipitation and soils that are generally more stable and fertile in this biome. This finding suggests that temperate forests could be particularly sensitive to shifts in temperature.

Tropical forests reflected a different picture, with all traits responding strongly to precipitation regime. Moreover, SLA and WD both showed the expected smaller effect of energy availability in the Neotropics compared to other biomes, with a stronger influence of precipitation and soil properties. Therefore, with changes in climate altered precipitation regimes and feedbacks on soils might be important limiting factors on forest functional composition in tropical forests.

4.4 | Species abundance

Weighting trait means by individual species abundances did not improve the strength of the trait-environment relationships, suggesting that only information on species presence at any given location is needed to investigate the distribution of functional traits of trees at broad scale. While surprising, this finding recurs in previous research conducted over smaller areas (Bjorkman et al., 2018; Dubuis et al., 2013; Pakeman et al., 2008), although it is rarely discussed. We have attempted to fill this gap by putting forward a hypothesis that merits further development. Dominant species are assumed to be at the optimum of their ecological niche and growing under favourable environmental conditions. Therefore, it is unlikely that a small change in the environment at the core of their distribution would cause a huge shift in their abundance and the functional composition of the forest, compared to rare species that are already growing under stressful conditions and may be displaced by other species with contrasting life strategies. Consistent with this hypothesis, the effect of the environment on tree functional traits was stronger at the edge of species distribution range (where a species is rare) than at the core in North America (Stahl et al., 2014). This indicates that the turnover in rare species might be coupled with shifts in functional composition. Community unweighted means, by giving more importance to the trait values of rare species, possibly increase the strength of the relationships between forest community trait composition and the environment.

4.5 | Limitations

Forest inventory protocols and sample plot sizes are not consistent across countries (Liang et al., 2022), which may lead to bias in the variance of projected data. As well, data coverage is uneven with tropical forests under and temperate forests overrepresented in both inventories and functional trait measurements. Increased sampling effort and funding to establish permanent sample plots in poorly documented areas are needed to rectify this discrepancy (Nesha et al., 2022). We acknowledge that additional variation in forest functional composition may be present due to genetic variation and phenotypic plasticity within species (Fridley et al., 2007; Fridley & Grime, 2010), especially in species-poor communities dominated by conifers (Anderegg et al., 2018; Siefert et al., 2015). This greater share of intraspecific variability may explain why our models in conifer-dominated boreal forests had generally less explanatory power (24%–31%) than in other biomes (26%–49%). The resolution of climatic (1 km^2) and edaphic variables (~250 m) prevented us from resolving very fine-grained variability at the scale of the local tree communities. Moreover, using averages for climatic conditions precluded getting data for the exact years of plots measurements and detecting possible effects of extreme climatic events (Waldock et al., 2018).

5 | CONCLUSION AND OUTLOOK

This study highlights several major trends in the distribution of tree functional traits. Wood density follows a latitudinal gradient aligned mostly with temperature, but other limiting factors (precipitation

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and soil properties) take a more important role within boreal and tropical forests. The links between wood density and precipitation regimes confirm the role of this trait in tree hydraulic safety globally. Our results demonstrate for the first time that worldwide, specific leaf area is more evenly influenced by major environmental gradients than traits linked to size, supporting the theory that this trait is involved in resource management. We show that its most acquisitive values are found in temperate forests, where leaf shedding is a ubiquitous process. Reproduction strategies are highly dependent on energy availability across the globe. Trees require large amount of energy to invest in their seeds, and to a lesser extent water, independent of soil properties.

In summary, forest community strategies are more conservative in stressful environments, but the limiting constraints that define these stressful environments, and thus the sensitivity of traits to environmental gradients, vary from biome to biome. This raises the question of the scale of study used to assess the response of community functional composition to global change. Tropical forests are a notable example, with greater importance on forest functional composition of gradients that are not captured by latitude, such as precipitation and soil properties, and whose effect can be confounded on a large scale. Future global studies should ensure that the heterogeneity of gradients and large vegetation groups across spatial scales are well captured.

Our results show that even at local community level, tree functions respond to broad environmental gradients. Further studies could investigate why the inclusion of species dominance does not improve these relationships compared to the mere presence of species in local forest communities. Furthermore, the importance of interactions among and between energy, soil properties and precipitation gradients indicates that the interplay of climate and soil is essential to understanding the distribution of trees' life strategies. Moving forward, models including interactions are essential to fully elucidate trait-environment relationships.

The large scope of this study, analysing over 148 trait–environment relationships, enabled us to test, illustrate and standardize results from the vast literature on trees' functional trait distribution, heterogeneous across different spatial scales and methodologies. These relationships can be used to guide future research into the sensitivity of forest communities to global change and how to integrate multiple aspects of the environment into large-scale modelling.

ACKNOWLEDGEMENTS

This work was funded in part by a Natural Sciences and Engineering Research Council of Canada Discovery Grant to Alain Paquette. This work was also made possible by the Global Forest Biodiversity Database (https://www.gfbinitiative.org/), which represents the work of over 200 independent investigators and their public and private funding agencies (see Appendix S13 Supplementary acknowledgements). The study was supported by the TRY initiative on plant traits (http://www.try-db.org). The TRY database is hosted at the Max Planck Institute for Biogeochemistry (MPI BGC, Germany) and supported by Future Earth and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig. We are thankful to Orane Mordacq and Cameron Daoust for their help in cleaning and processing the data as well as collecting functional trait values from literature, and Charlotte Langlois, Marine Fernandez and Maxime Paquette for preparing the manuscript. We would like to thank François Rousseu, Daniel Schoenig, Daniel Lesieur and Mélanie Desrochers, CFR professionals in statistics, database management and GIS.

FUNDING INFORMATION

Natural Sciences and Engineering Research Council of Canada.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interests.

DATA AVAILABILITY STATEMENT

Data on community means of traits as well as climatic and pedologic variables are available through figshare: https://figshare.com/ Information regarding variable selection and model outputs is available as Supplementary material. The GFBI database is available upon written request at https://www.gfbinitiative.org/datarequest. The TRY database is available upon written request at https://www.try-db.org/TryWeb/Prop0.php Any other relevant data are available from the corresponding authors upon reasonable request.

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BIOSKETCH

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SUPPORTING INFORMATION

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How to cite this article: Bouchard, E., Searle, E. B., Drapeau, P., Liang, J., Gamarra, J. G. P., Abegg, M., Alberti, G., Zambrano, A. A., Alvarez-Davila, E., Alves, L. F., Avitabile, V., Aymard, G., Bastin, J.-F., Birnbaum, P., Bongers, F., Bouriaud, O., Brancalion, P., Broadbent, E., Bussotti, F., … Paquette, A. (2024). Global patterns and environmental drivers of forest functional composition. *Global Ecology and Biogeography*, *33*, 303–324. https://doi.org/10.1111/geb.13790

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APPENDIX 1

DATA SOURCES

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