

# Global patterns and environmental drivers of forest functional composition

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**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 (Bruehlheide et al., 2018; Moles et al., 2014; Šimová et al., 2015; Swenson et al., 2012; Swenson & Enquist, 2007; Swenson & Weiser, 2010; Wieczynski et al., 2019), thereby assuming that one environmental variable

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; Šimová 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

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 & Quedsted, 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<sup>2</sup> 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

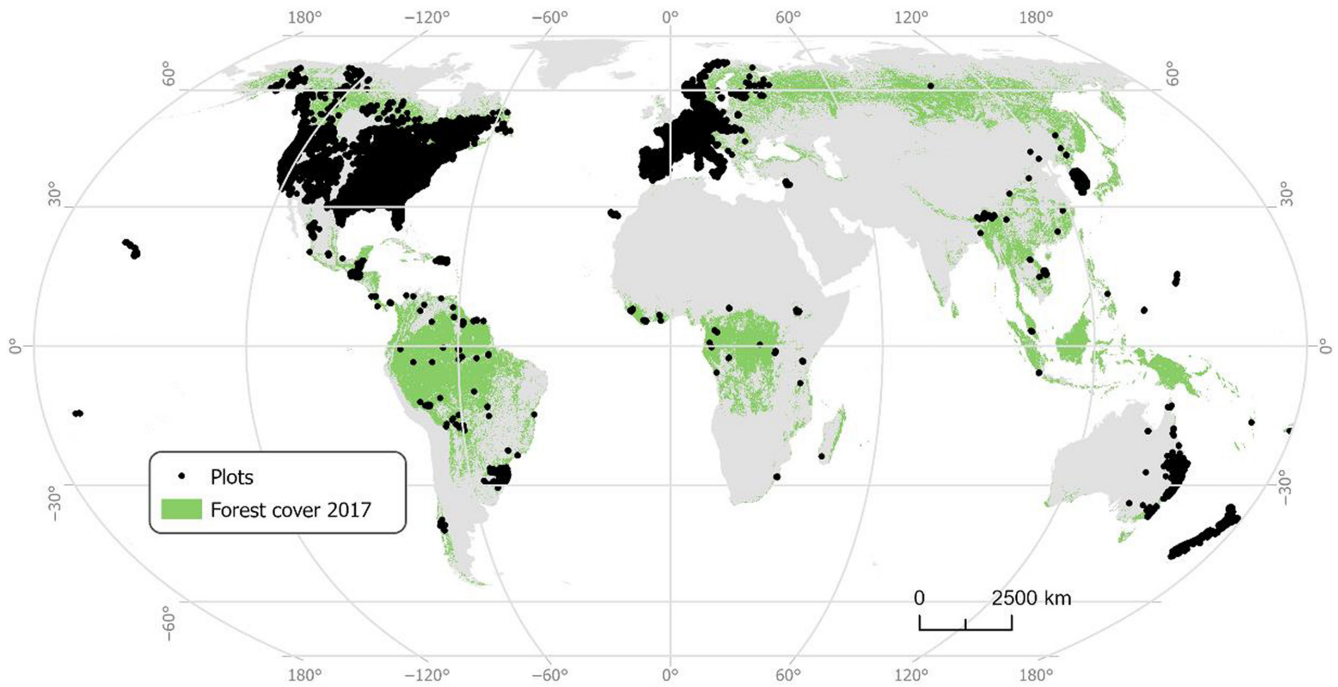
in raw data between traits and environmental variables. We built four models per trait with data fitted at different scales and biomes: global forests (all data), boreal forests, temperate forests and tropical forests. Biome-related results were obtained using biome-level models trained on data coming 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.

Functional traits	Taxonomy				Number of plots			
	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



**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
<i>Functional traits</i>				
Wood density	WD	mg/mm <sup>3</sup>	0.15 to 1.24	0.55
Specific leaf area	SLA	m <sup>2</sup> /kg	1.3 to 169.8	16.4
Seed mass	SM	mg	0.01 to 576,800	860
<i>Environmental variables</i>				
<i>Energy gradient</i>				
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 <sup>2</sup> *day	7296 to 21,786	14,369
<i>Precipitation gradient</i>				
Annual precipitation	AP	mm	68 to 4712	1175
Precipitation seasonality	PS		5.5 to 120.2	26
<i>Soil properties gradient</i>				
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 <sup>3</sup>	606.5 to 1696.2	1320.4

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

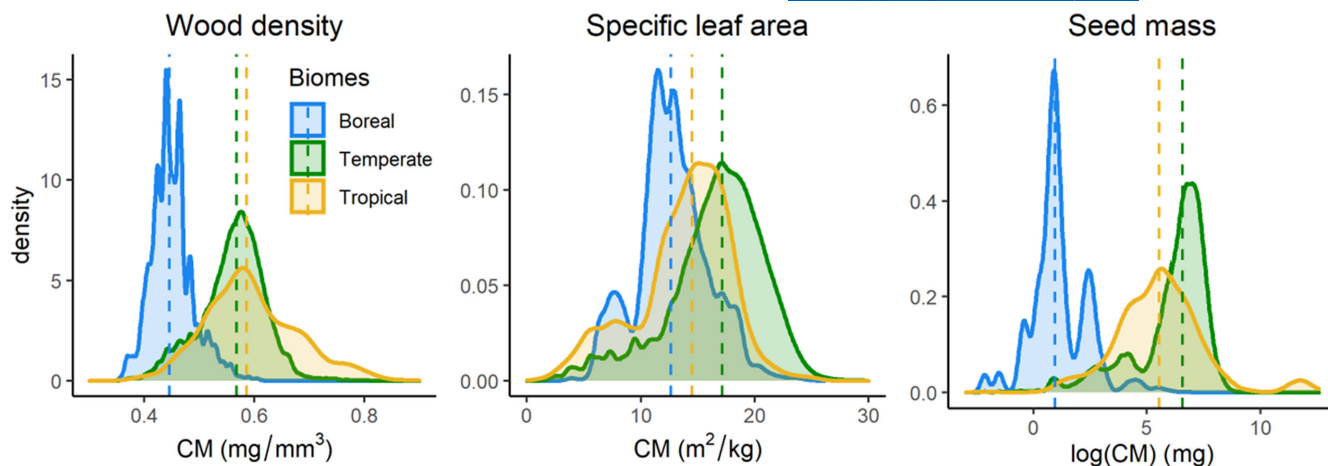


FIGURE 2 Density plots of community unweighted means (CM) per trait and biome. The dashed lines display the median of the distribution.

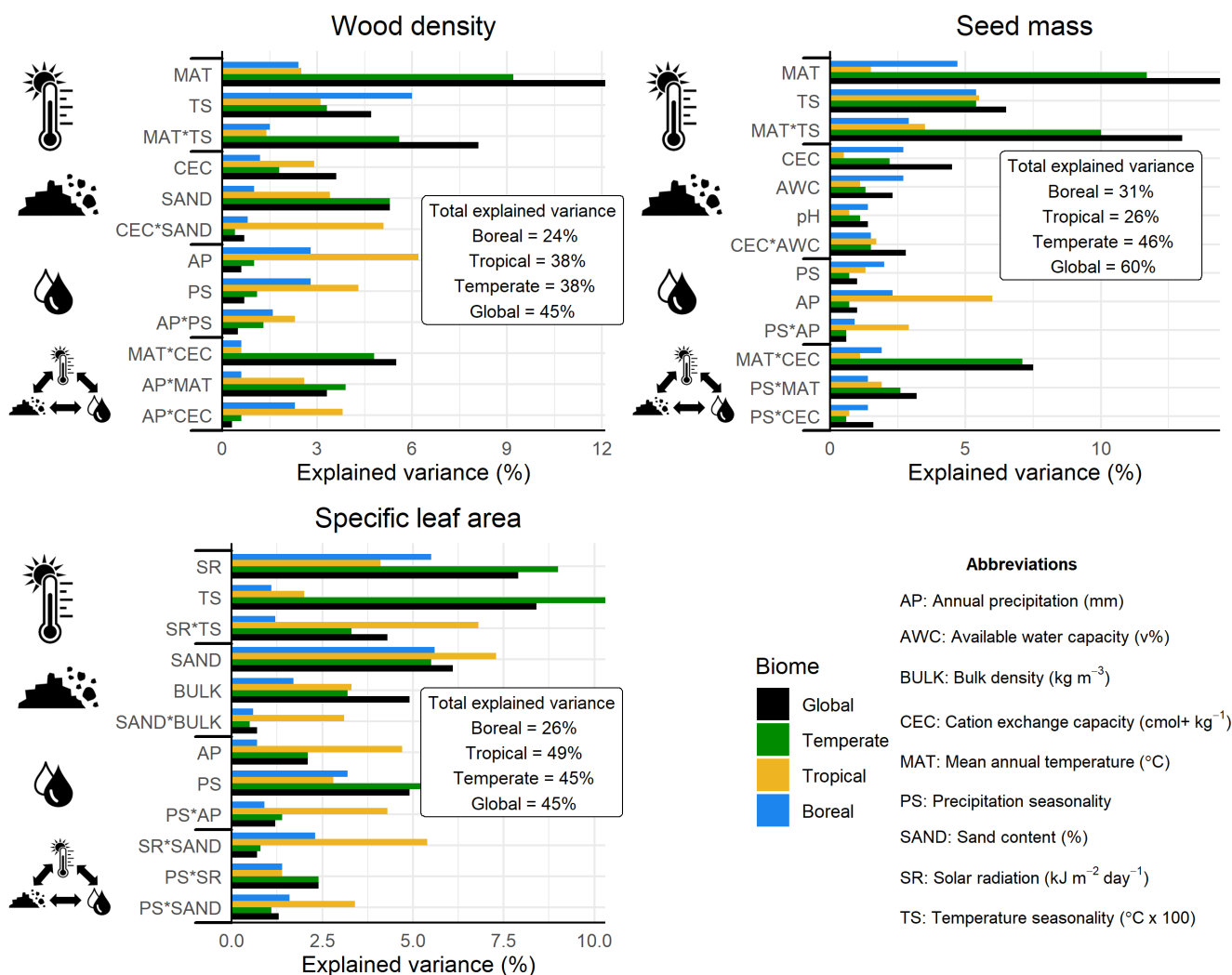
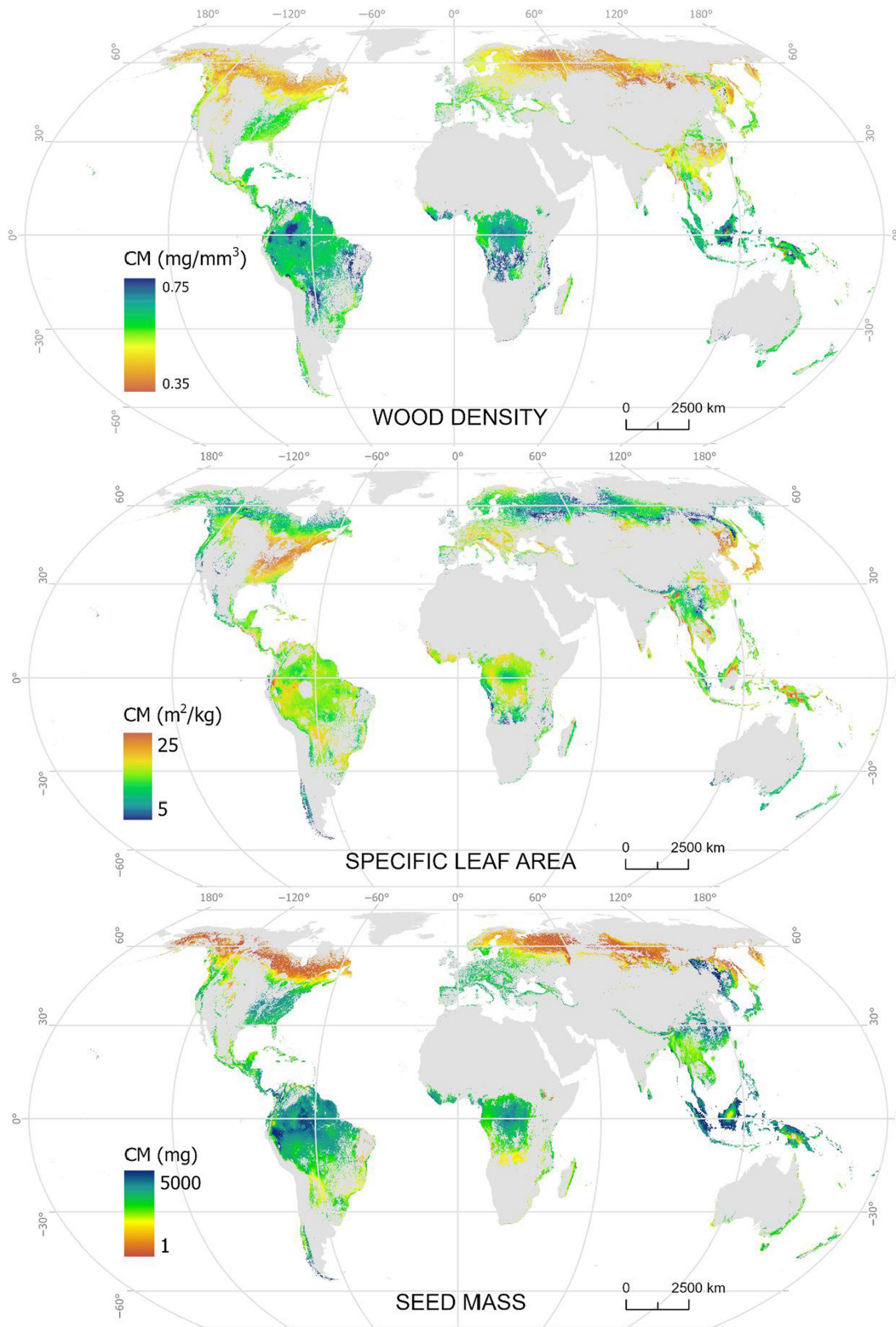


FIGURE 3 Results of variance partitioning from dominance analysis. Bar colours represent different models (boreal, tropical, temperate, global), whereas pictograms on the y axis emphasize the gradient to which the variables belong (energy availability, soil properties, precipitation or an interaction 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.



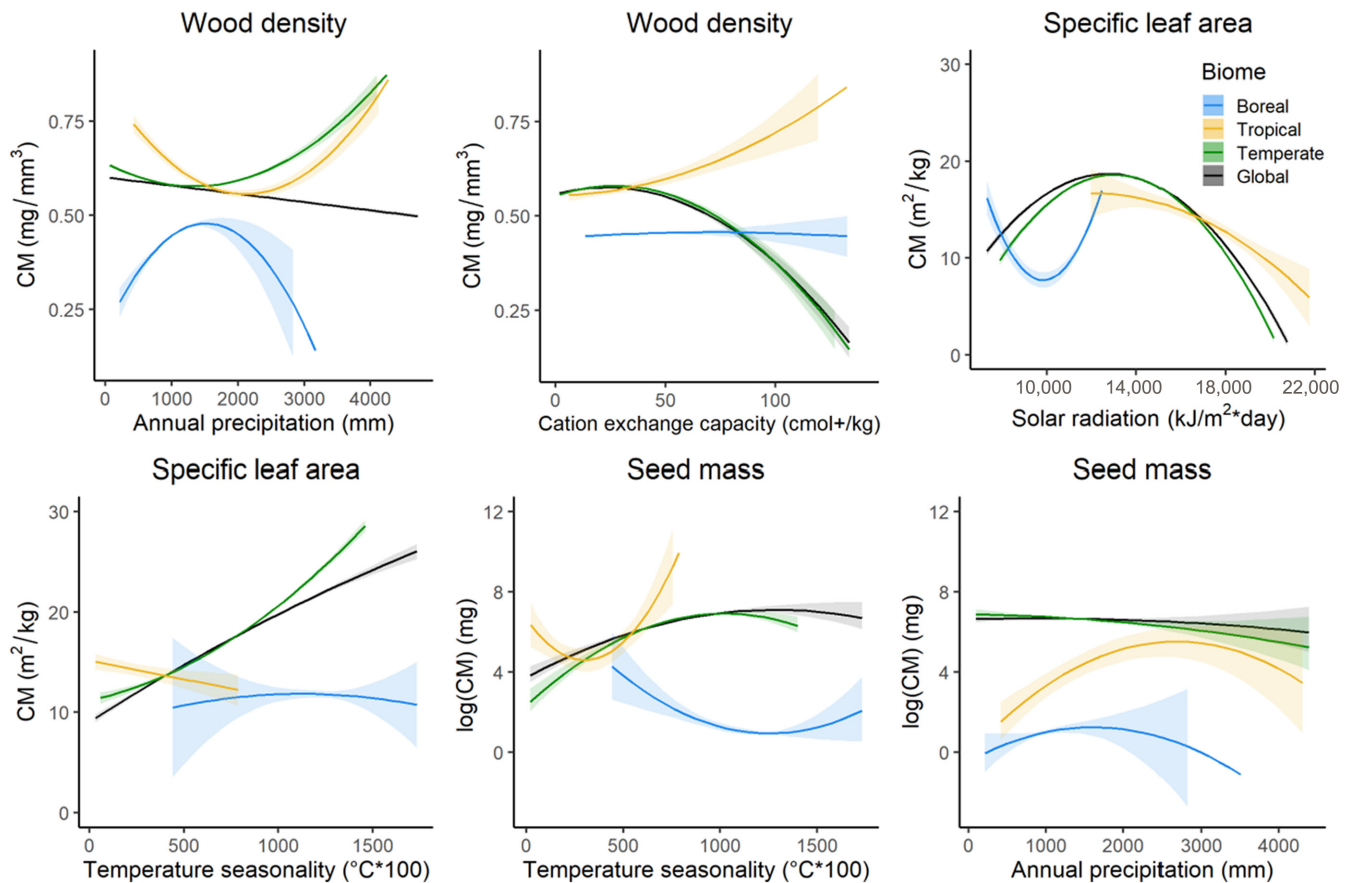
**FIGURE 4** Biogeographical representations of the explained distribution of functional traits of trees. The colour palette represents a gradient from acquisitive strategies (red-yellow) to conservative strategies (green-blue). Map projection, WGS 1984 Equal Earth (world).

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





**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

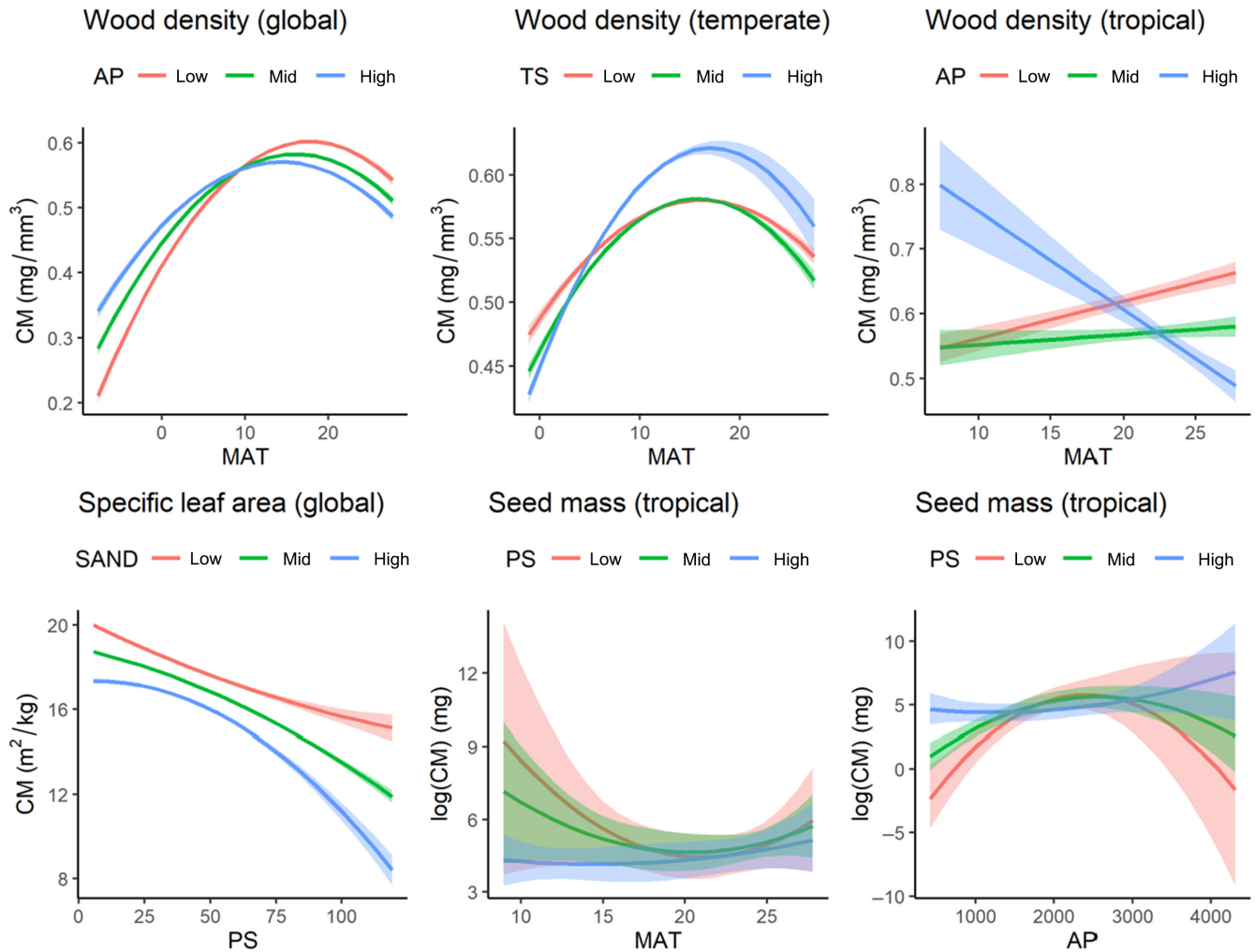
### 4.1 | Global patterns

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



**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  $13,000 \text{ kJ m}^{-2} \text{ day}^{-1}$ ). Conservative strategies of WD and SM reached an optimum at mean annual temperatures around  $15^\circ\text{C}$ , 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; Wiczyński 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

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 ( $\pm 0.01$  mg/mm<sup>3</sup> 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; Šimová 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

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 (Bruehlheide 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; Wiczyński 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

(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<sup>2</sup>) 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

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.

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## 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/datarquest>. 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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- de la Riva, E. G., Violle, C., Pérez-Ramos, I. M., Marañón, T., Navarro-Fernández, C. M., Olmo, M., & Villar, R. (2018). A multidimensional functional trait approach reveals the imprint of environmental stress in Mediterranean Woody Communities. *Ecosystems*, 21(2), 248–262. <https://doi.org/10.1007/s10021-017-0147-7>
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönsch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171. <https://doi.org/10.1038/nature16489>
- Dubuis, A., Rossier, L., Pottier, J., Pellissier, L., Vittoz, P., & Guisan, A. (2013). Predicting current and future spatial community patterns of plant functional traits. *Ecography*, 36(11), 1158–1168. <https://doi.org/10.1111/j.1600-0587.2013.00237.x>
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315. <https://doi.org/10.1002/joc.5086>
- Fortunel, C., Paine, C. E. T., Fine, P. V. A., Kraft, N. J. B., & Baraloto, C. (2014). Environmental factors predict community functional composition in Amazonian forests. *Journal of Ecology*, 102(1), 145–155. <https://doi.org/10.1111/1365-2745.12160>
- Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Fridley, J. D., & Grime, J. P. (2010). Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology*, 91(8), 2272–2283.
- Fridley, J. D., Grime, J. P., & Bilton, M. (2007). Genetic identity of interspecific neighbours mediates plant responses to competition and environmental variation in a species-rich grassland. *Journal of Ecology*, 95(5), 908–915. <https://doi.org/10.1111/j.1365-2745.2007.01256.x>
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M. C., Fröberg, M., Stendahl, J., Philipson, C. D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., & Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, 4, 1340. <https://doi.org/10.1038/ncomms2328>
- Garnier, E., Cortez, J., Billès, G., Navas, M. L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J. P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85(9), 2630–2637. <https://doi.org/10.1890/03-0799>
- Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., & Schepaschenko, D. G. (2015). Boreal forest health and global change. *Science*, 349(6250), 819–822. <https://doi.org/10.1126/science.aaa9092>
- Gong, H., & Gao, J. (2019). Soil and climatic drivers of plant SLA (specific leaf area). *Global Ecology and Conservation*, 20, e00696. <https://doi.org/10.1016/j.gecco.2019.e00696>
- Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C. D., Fensham, R., Laughlin, D. C., Kattge, J., Bönsch, G., Kraft, N. J. B., & Jump, A. S. (2017). Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters*, 20(4), 539–553. <https://doi.org/10.1111/ele.12748>
- Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, 111(982), 40–1194. <https://doi.org/10.1086/283244>
- Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, 86(6), 902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>
- Hacke, U. G., Sperry, J. S., Pockman, W. T., Davis, S. D., & McCulloh, K. A. (2001). Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, 126(4), 457–461. <https://doi.org/10.1007/s004420100628>
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., & Townshend, J. R. G. (2013). High-resolution global maps of 21st-century Forest cover change. *Science*, 342(6160), 850–853. <https://doi.org/10.1126/science.1239552>
- Hengl, T., De Jesus, J. M., Heuvelink, G. B. M., Gonzalez, M. R., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M. N., Geng, X., Bauer-Marschallinger, B., Guevara, M. A., Vargas, R., MacMillan, R. A., Batjes, N. H., Leenaars, J. G. B., Ribeiro, E., Wheeler, I., Mantel, S., & Kempen, B. (2017). SoilGrids250m: Global gridded soil information based on machine learning. *PLoS ONE*, 12(2), 1–40. <https://doi.org/10.1371/journal.pone.0169748>
- Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American Naturalist*, 163(2), 192–211. <https://doi.org/10.1086/381004>
- Holdridge, L. R. (1947). Determination of world plant formations from simple climatic data. *Science*, 105(2727), 367–368. <https://doi.org/10.1126/science.105.2727.367>
- Joswig, J. S., Wirth, C., Schuman, M. C., Kattge, J., Reu, B., Wright, I. J., Sippel, S. D., Rüger, N., Richter, R., Schaepman, M. E., van Bodegom, P. M., Cornelissen, J. H. C., Díaz, S., Hattigh, W. N., Kramer, K., Lens, F., Niinemets, Ü., Reich, P. B., Reichstein, M., ... Mahecha, M. D. (2022). Climatic and soil factors explain the two-dimensional spectrum of global plant trait variation. *Nature Ecology and Evolution*, 6(1), 36–50. <https://doi.org/10.1038/s41559-021-01616-8>
- Kattge, J., Bönsch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., & Acosta, A. T. (2020). TRY plant trait database—enhanced coverage and open access. *Global Change Biology*, 26(1), 119–188. <https://doi.org/10.1111/gcb.14904>
- Keppel, G., Craven, D., Weigelt, P., Smith, S. A., van der Sande, M. T., Sandel, B., Levin, S. C., Kreft, H., & Knight, T. M. (2021). Synthesizing tree biodiversity data to understand global patterns and processes of vegetation. *Journal of Vegetation Science*, 32(3), e13021. <https://doi.org/10.1111/jvs.13021>
- Kerkhoff, A. J., & Enquist, B. J. (2009). Multiplicative by nature: Why logarithmic transformation is necessary in allometry. *Journal of Theoretical Biology*, 257(3), 519–521. <https://doi.org/10.1016/j.jtbi.2008.12.026>
- Kricher, J. C. (2017). The new neotropical companion. In *The new neotropical companion*. Princeton University Press.
- Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology*, 73(6), 1943–1967. <https://doi.org/10.2307/1941447>
- Liang, J., Gamarra, J. G. P., Picard, N., Zhou, M., Pijanowski, B., Jacobs, D. F., Reich, P. B., Crowther, T. W., Nabuurs, G.-J., de Miguel, S., Fang, J., Woodall, C. W., Svenning, J.-C., Jucker, T., Bastin, J.-F., Wiser, S. K., Slik, F., Hérault, B., Alberti, G., ... Hui, C. (2022). Co-limitation towards lower latitudes shapes global forest diversity gradients. *Nature Ecology & Evolution*, 6, 1423–1437. <https://doi.org/10.1038/s41559-022-01831-x>
- Lord, J., Egan, J., Clifford, T., Jurado, E., Leishman, M., Williams, D., & Westoby, M. (1997). Larger seeds in tropical floras: Consistent patterns independent of growth form and dispersal mode. *Journal of Biogeography*, 24(2), 205–211. <https://doi.org/10.1046/j.1365-2699.1997.00126.x>
- Maire, V., Wright, I. J., Prentice, I. C., Batjes, N. H., Bhaskar, R., van Bodegom, P. M., Cornwell, W. K., Ellsworth, D., Niinemets, Ü., Ordóñez, A., Reich, P. B., & Santiago, L. S. (2015). Global effects of soil and climate on leaf photosynthetic traits and rates. *Global Ecology and Biogeography*, 24(6), 706–717. <https://doi.org/10.1111/geb.12296>
- Malhado, A. C. M., Oliveira-Neto, J. A., Stropp, J., Strona, G., Dias, L. C. P., Pinto, L. B., & Ladle, R. J. (2015). Climatological correlates of seed size in Amazonian forest trees. *Journal of Vegetation Science*, 26(5), 956–963. <https://doi.org/10.1111/jvs.12301>



- Maynard, D. S., Bialic-Murphy, L., Zohner, C. M., Averill, C., van den Hoogen, J., Ma, H., Mo, L., Smith, G. R., Acosta, A. T. R., Aubin, I., Berenguer, E., Boonman, C. C. F., Catford, J. A., Cerabolini, B. E. L., Dias, A. S., González-Melo, A., Hietz, P., Lusk, C. H., Mori, A. S., ... Crowther, T. W. (2022). Global relationships in tree functional traits. *Nature Communications*, 13(1), 1–12. <https://doi.org/10.1038/s41467-022-30888-2>
- Moles, A. T. (2017). Being John Harper: Using evolutionary ideas to improve understanding of global patterns in plant traits. *Journal of Ecology*, 106(1), 1–18. <https://doi.org/10.1111/1365-2745.12887>
- Moles, A. T., Ackerly, D. D., Tweddle, J. C., Dickie, J. B., Smith, R., Leishman, M. R., Mayfield, M. M., Pitman, A., Wood, J. T., & Westoby, M. (2007). Global patterns in seed size. *Global Ecology and Biogeography*, 16, 109–116. <https://doi.org/10.1111/j.1466-822x.2006.00259.x>
- Moles, A. T., Perkins, S. E., Laffan, S. W., Flores-Moreno, H., Awasthy, M., Tindall, M. L., Sack, L., Pitman, A., Kattge, J., Aarssen, L. W., Anand, M., Bahn, M., Blonder, B., Cavender-Bares, J., Cornelissen, J. H. C., Cornwell, W. K., Díaz, S., Dickie, J. B., Freschet, G. T., ... Bonser, S. P. (2014). Which is a better predictor of plant traits: Temperature or precipitation? *Journal of Vegetation Science*, 25(5), 1167–1180. <https://doi.org/10.1111/jvs.12190>
- Moles, A. T., Westoby, M., & Eriksson, O. (2006). Seed size and plant strategy across the whole life cycle. *Oikos*, 113(1), 91–105. <https://doi.org/10.1111/j.0030-1299.2006.14194.x>
- Nesha, K., Herold, M., De Sy, V., de Bruin, S., Araza, A., Málaga, N., Gamarra, J. G. P., Hergoualc'h, K., Pekkarinen, A., Ramirez, C., Morales-Hidalgo, D., & Tavani, R. (2022). Exploring characteristics of national forest inventories for integration with global space-based forest biomass data. *Science of the Total Environment*, 850, 157788. <https://doi.org/10.1016/j.scitotenv.2022.157788>
- O'Brien, M. J., Engelbrecht, B. M. J., Joswig, J., Pereyra, G., Schuldt, B., Jansen, S., Kattge, J., Landhäusser, S. M., Levick, S. R., Preisler, Y., Väänänen, P., & Macinnis-Ng, C. (2017). A synthesis of tree functional traits related to drought-induced mortality in forests across climatic zones. *Journal of Applied Ecology*, 54(6), 1669–1686. <https://doi.org/10.1111/1365-2664.12874>
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on earth. *Bioscience*, 51(11), 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:teotwa\]2.0.co;2](https://doi.org/10.1641/0006-3568(2001)051[0933:teotwa]2.0.co;2)
- Ordoñez, J. C., Van Bodegom, P. M., Witte, J.-P. M., Wright, I. J., Reich, P. B., & Aerts, R. (2009). A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography*, 18(2), 137–149. <https://doi.org/10.1111/j.1466-8238.2008.00441.x>
- Pakeman, R. J., Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Doležal, J., Eriksson, O., Freitas, H., Golodets, C., Kigel, J., Kleyer, M., Lepš, J., Meier, T., Papadimitriou, M., Papanastasis, V. P., Queded, H., Quétier, F., Rusch, G., ... Vile, D. (2008). Impact of abundance weighting on the response of seed traits to climate and land use. *Journal of Ecology*, 96(2), 355–366. <https://doi.org/10.1111/j.1365-2745.2007.01336.x>
- Pakeman, R. J., & Queded, H. M. (2007). Sampling plant functional traits: What proportion of the species need to be measured? *Applied Vegetation Science*, 10(1), 91–96. <https://doi.org/10.1111/j.1654-109x.2007.tb00507.x>
- Pebesma, E., & Heuvelink, G. (2016). Spatio-temporal interpolation using gstat. *RFID Journal*, 8(1), 204–218. <https://doi.org/10.32614/rj-2016-014>
- Pebesma, E. J. (2004). Multivariable geostatistics in S: The gstat package. *Computers & Geosciences*, 30(7), 683–691. <https://doi.org/10.1016/j.cageo.2004.03.012>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, J. H. (2016). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 64(8), 715–716. [https://doi.org/10.1071/BT12225\\_CO](https://doi.org/10.1071/BT12225_CO)
- Pinho, B. X., Tabarelli, M., Braak, C. J. F., Wright, S. J., Arroyo-Rodríguez, V., Benchimol, M., Engelbrecht, B. M. J., Pierce, S., Hietz, P., Santos, B. A., Peres, C. A., Müller, S. C., Wright, I. J., Bongers, F., Lohbeck, M., Niinemets, Ü., Slot, M., Jansen, S., Jamelli, D., ... Melo, F. P. L. (2021). Functional biogeography of neotropical moist forests: Trait-climate relationships and assembly patterns of tree communities. *Global Ecology and Biogeography*, 30(7), 1430–1446. <https://doi.org/10.1111/geb.13309>
- Ploton, P., Mortier, F., Réjou-Méchain, M., Barbier, N., Picard, N., Rossi, V., Dormann, C., Cornu, G., Viennois, G., Bayol, N., Lyapustin, A., Gourlet-Fleury, S., & Péliissier, R. (2020). Spatial validation reveals poor predictive performance of large-scale ecological mapping models. *Nature Communications*, 11(1), 4540. <https://doi.org/10.1038/s41467-020-18321-y>
- Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist*, 182(3), 565–588. <https://doi.org/10.1111/j.1469-8137.2009.02830.x>
- Preston, K. A., Cornwell, W. K., & DeNoyer, J. L. (2006). Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytologist*, 170(4), 807–818. <https://doi.org/10.1111/j.1469-8137.2006.01712.x>
- R Core Team. (2020). R: A language and environment for statistical computing. <https://www.R-project.org/>
- Réjou-Méchain, M., Mortier, F., Bastin, J. F., Cornu, G., Barbier, N., Bayol, N., Bénédet, F., Bry, X., Dauby, G., Deblauwe, V., Doucet, J. L., Doumenge, C., Fayolle, A., Garcia, C., Kibambe Lubamba, J. P., Loumeto, J. J., Ngomanda, A., Ploton, P., Sonké, B., ... Gourlet-Fleury, S. (2021). Unveiling African rainforest composition and vulnerability to global change. *Nature*, 593(7857), 90–94. <https://doi.org/10.1038/s41586-021-03483-6>
- Sedio, B. E., Parker, J. D., McMahon, S. M., & Wright, A. S. J. (2018). Comparative foliar metabolomics of a tropical and a temperate forest community. *Ecology*, 99(12), 2647–2653. <https://doi.org/10.1002/ecy.2533>
- Shipley, B., Laughlin, D. C., Sonnier, G. G., & Otfinowski, R. (2011). A strong test of a maximum entropy model of trait-based community assembly. *Ecology*, 92(2), 507–517. <https://doi.org/10.1890/10-0394.1>
- Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., de L. Dantas, V., de Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., ... Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18, 1406–1419. <https://doi.org/10.1111/ele.12508>
- Šimová, I., Violle, C., Kraft, N. J. B., Storch, D., Svenning, J. C., Boyle, B., Donoghue, J. C., Jørgensen, P., McGill, B. J., Morueta-Holme, N., Piel, W. H., Peet, R. K., Regetz, J., Schildhauer, M., Spencer, N., Thiers, B., Wiser, S., & Enquist, B. J. (2015). Shifts in trait means and variances in north American tree assemblages: Species richness patterns are loosely related to the functional space. *Ecography*, 38(7), 649–658. <https://doi.org/10.1111/ecog.00867>
- Simpson, A. H., Richardson, S. J., & Laughlin, D. C. (2016). Soil-climate interactions explain variation in foliar, stem, root and reproductive traits across temperate forests. *Global Ecology and Biogeography*, 25(8), 964–978. <https://doi.org/10.1111/geb.12457>
- Stahl, U., Kattge, J., Reu, B., Voigt, W., Ogle, K., Dickie, J., & Wirth, C. (2013). Whole-plant trait spectra of North American woody plant species reflect fundamental ecological strategies. *Ecosphere*, 4(10), 1–28. <https://doi.org/10.1890/ES13-00143.1>

- Stahl, U., Reu, B., & Wirth, C. (2014). Predicting species' range limits from functional traits for the tree flora of North America. *Proceedings of the National Academy of Sciences of the United States of America*, 111(38), 13739–13744. <https://doi.org/10.1073/pnas.1300673111>
- Suzuki, R., Xu, J., & Motoya, K. (2006). Global analyses of satellite-derived vegetation index related to climatological wetness and warmth. *International Journal of Climatology*, 26(4), 425–438. <https://doi.org/10.1002/joc.1256>
- Swenson, N. G., & Enquist, B. J. (2007). Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, 94(3), 451–459. <https://doi.org/10.3732/ajb.94.3.451>
- Swenson, N. G., Enquist, B. J., Pither, J., Kerkhoff, A. J., Boyle, B., Weiser, M. D., Elser, J. J., Fagan, W. F., Forero-Montaña, J., Fyllas, N., Kraft, N. J. B., Lake, J. K., Moles, A. T., Patiño, S., Phillips, O. L., Price, C. A., Reich, P. B., Quesada, C. A., Stegen, J. C., ... Nolting, K. M. (2012). The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography*, 21(8), 798–808. <https://doi.org/10.1111/j.1466-8238.2011.00727.x>
- Swenson, N. G., & Weiser, M. D. (2010). Plant geography upon the basis of functional traits: An example from eastern North American trees. *Ecology*, 91(8), 2234–2241. <https://doi.org/10.1890/09-1743>
- Ter Steege, H., Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., Molino, J. F., Prévost, M. F., Spichiger, R., Castellanos, H., Von Hildebrand, P., & Vásquez, R. (2006). Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*, 443(7110), 444–447. <https://doi.org/10.1038/nature05134>
- Terborgh, J. (1973). On the notion of favorableness in plant ecology. *The American Naturalist*, 107(956), 481–501. <https://doi.org/10.1086/282852>
- Valavi, R., Elith, J., Lahoz-Monfort, J. J., & Guillerá-Arroita, G. (2019). blockCV: An R package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models. *Methods in Ecology and Evolution*, 10(2), 225–232. <https://doi.org/10.1111/2041-210X.13107>
- Villar, R., & Merino, J. (2001). Comparison of leaf construction costs in woody species with differing leaf life-spans in contrasting ecosystems. *New Phytologist*, 151(1), 213–226. <https://doi.org/10.1046/j.1469-8137.2001.00147.x>
- Vleminckx, J., Fortunel, C., Valverde-Barrantes, O., Timothy Paine, C. E., Engel, J., Petronelli, P., Dourdain, A. K., Guevara, J., Bérroujon, S., & Baraloto, C. (2021). Resolving whole-plant economics from leaf, stem and root traits of 1467 Amazonian tree species. *Oikos*, 130(7), 1193–1208. <https://doi.org/10.1111/oik.08284>
- Waldock, C., Dornelas, M., & Bates, A. E. (2018). Temperature-driven biodiversity change: Disentangling space and time. *Bioscience*, 68(11), 873–884. <https://doi.org/10.1093/biosci/biy096>
- Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199(2), 213–227. <https://doi.org/10.1023/A:1004327224729>
- Wieczynski, D. J., Boyle, B., Buzzard, V., Duran, S. M., Henderson, A. N., Hulshof, C. M., Kerkhoff, A. J., McCarthy, M. C., Michaletz, S. T., Swenson, N. G., Asner, G. P., Bentley, L. P., Enquist, B. J., & Savage, V. M. (2019). Climate shapes and shifts functional biodiversity in forests worldwide. *Proceedings of the National Academy of Sciences*, 116(2), 587–592. <https://doi.org/10.6084/m9.figshare.7436951.v1>
- Wiemann, M. C., & Williamson, G. B. (2002). Geographic variation in wood specific gravity: Effects of latitude, temperature, and precipitation. *Wood and Fiber Science*, 34(1), 97–107.
- Wigley, B. J., Slingsby, J. A., Díaz, S., Bond, W. J., Fritz, H., & Coetsee, C. (2016). Leaf traits of African woody savanna species across climate and soil fertility gradients: Evidence for conservative versus acquisitive resource-use strategies. *Journal of Ecology*, 104(5), 1357–1369. <https://doi.org/10.1111/1365-2745.12598>
- Wilson, P. J., Thompson, K., & Hodgson, J. G. (1999). Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist*, 143(1), 155–162. <https://doi.org/10.1046/j.1469-8137.1999.00427.x>
- Wright, I. J., Reich, P. B., Cornelissen, J. H. C., Falster, D. S., Groom, P. K., Hikosaka, K., Lee, W., Lusk, C. H., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Warton, D. I., & Westoby, M. (2005). Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography*, 14(5), 411–421. <https://doi.org/10.1111/j.1466-822x.2005.00172.x>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827. <https://doi.org/10.1038/nature02403>
- Zhang, S.-B., Cao, K.-F., Fan, Z.-X., & Zhang, J.-L. (2013). Potential hydraulic efficiency in angiosperm trees increases with growth-site temperature but has no trade-off with mechanical strength. *Global Ecology and Biogeography*, 22(8), 971–981. <https://doi.org/10.1111/geb.12056>
- Zhang, S.-B., Ferry Slik, J. W., Zhang, J.-L., & Cao, K.-F. (2011). Spatial patterns of wood traits in China are controlled by phylogeny and the environment. *Global Ecology and Biogeography*, 20(2), 241–250. <https://doi.org/10.1111/j.1466-8238.2010.00582.x>

## BIOSKETCH

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## SUPPORTING INFORMATION

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## APPENDIX 1

## DATA SOURCES

- Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C., & Franco, M. (2014). Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences*, 111(2), 740–745.
- Atkin, O. K., Bloomfield, K. J., Reich, P. B., Tjoelker, M. G., Asner, G. P., Bonal, D., Bönisch, G., Bradford, M., Cernusak, L. A., Cosio, E. G., Creek, D., Crous, K. Y., Domingues, T., Dukes, J. S., Egerton, J. J. G., Evans, J. R., Farquhar, G. D., Fyllas, N. M., Gauthier, P. P. G., ... Zaragoza-Castells, J. (2015). Global variability in leaf respiration among plant functional types in relation to climate and leaf traits. *New Phytologist*. <https://doi.org/10.1111/nph.13253>
- Atkin, O. K., Schortemeyer, M., McFarlane, N., & Evans, J. R. (1999). The response of fast- and slow-growing acacia species to elevated atmospheric CO<sub>2</sub>: An analysis of the underlying components of relative growth rate. *Oecologia*, 120, 544–554.
- Auger, S., & Shipley, B. (2012). Interspecific and intraspecific trait variation along short environmental gradients in an old-growth temperate forest. *Journal of Vegetation Science*. [10.1111/j.1654-1103.2012.01473.x](https://doi.org/10.1111/j.1654-1103.2012.01473.x)
- Baraloto, C., Paine, C. E. T., Poorter, L., Beuchene, J., Bonal, D., Domenach, A.-M., Hérault, B., Patino, S., Roggy, J.-C., & Chave, J. (2010). Decoupled leaf and stem economics in rainforest trees. *Ecology Letters*, 13, 1338–1347.
- Blonder, B., Buzzard, B., Sloat, L., Simova, I., Lipson, R., Boyle, B., & Enquist, B. (2012). The shrinkage effect biases estimates of paleoclimate. *American Journal of Botany*, 99(11), 1756–1763.
- Blonder, B., Violle, C., & Enquist, B. J. (2013). Assessing the causes and scales of the leaf economics spectrum using venation networks in *Populus tremuloides*. *Journal of Ecology*, 101, 981–989. <https://doi.org/10.1111/1365-2745.12102>
- Blonder, B., Violle, C., Patrick, L., & Enquist, B. (2011). Leaf venation networks and the origin of the leaf economics spectrum. *Ecology Letters*, 14(2), 91–100.
- Bocanegra-González, K. T., Fernandez-Mendez, F., & Galvis-Jiménez, J. F. (2013). *Determinación de la resiliencia en bosques secundarios húmedos tropicales a través de la diversidad funcional de árboles en la región del Bajo Calima*. Tesis, Universidad del Tolima, Facultad de Ingeniería Forestal, Ibagué.
- Bond-Lamberty, B., Wang, C., & Gower, S. T. (2002). Leaf area dynamics of a boreal black spruce fire chronosequence. *Tree Physiology*, 22(14), 993–1001.
- Brown, K. A., Flynn, D. F. B., Abram, N. K., Ingram, J. C., Johnson, S. E., & Wright, P. (2011). Assessing natural resource use by forest-reliant communities in Madagascar using functional diversity and functional redundancy metrics. *PLoS ONE*, 6(9), e24107. <https://doi.org/10.1371/journal.pone.0024107>
- Burrascano, S., Copiz, R., Del Vico, E., Fagiani, S., Giarrizzo, E., Mei, M., Mortelliti, A., Sabatini, F. M., & Blasi, C. (2015). Wild boar rooting intensity determines shifts in understory composition and functional traits. *Community Ecology*, 16(2), 244–253. <https://doi.org/10.1556/168.2015.16.2.12>
- Butterfield, B. J., & Briggs, J. M. (2011). Regeneration niche differentiates functional strategies of desert woody plant species. *Oecologia*, 165, 477–487.
- Byun, C., de Blois, S., & Brisson, J. (2013). Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.12016>
- Campbell, C., Atkinson, L., Zaragoza-Castells, J., Lundmark, M., Atkin, O., & Hurry, V. (2007). Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional group. *New Phytologist*, 176, 375–389.
- Campetella, G., Botta-Dukát, Z., Wellstein, C., Canullo, R., Gatto, S., Chelli, S., Mucina, L., & Bartha, S. (2011). Patterns of plant trait-environment relationships along a forest succession chronosequence. *Agriculture, Ecosystems & Environment*, 145(1), 38–48. <https://doi.org/10.1016/j.agee.2011.06.025>
- Carswell, F. E., Meir, P., Wandelli, E. V., Bonates, L. C. M., Kruijt, B., Barbosa, E. M., Nobre, A. D., & Jarvis, P. G. (2000). Photosynthetic capacity in a central Amazonian rain forest. *Tree Physiology*, 20(3), 179–186. 8 p.
- Castro-Diez, P., Puyravaud, J. P., Cornelissen, J. H. C., & Villar-Salvador, P. (1998). Stem anatomy and relative growth rate in seedlings of a wide range of woody plant species and types. *Oecologia*, 116, 57–66.
- Catford, J. A., Morris, W. K., Vesk, P. A., Gippel, C. J., & Downes, B. J. (2014). Species and environmental characteristics point to flow regulation and drought as drivers of riparian plant invasion. *Diversity and Distributions*, 20, 1084–1096. <https://doi.org/10.1111/ddi.12225>
- Cavender-Bares, J., Keen, A., & Miles, B. (2006). Phylogenetic structure of floridian plant communities depends on taxonomic and spatial scale. *Ecology*, 87, S109–S122.
- Chacón-Madriral, E., Wolfgang, W., Hietz, P., & Dullinger, S. A stress-tolerance syndrome distinguishes endemic tropical trees from their widespread congeners. Unpublished.
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12, 351–366.
- Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J., Feild, T. S., Gleason, S. M., Hacke, U. G., Jacobsen, A. L., Lens, F., Maherali, H., Martinez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J., Nardini, A., Jarmila Pittermann, R., ... Zanne, A. E. (2012). Global convergence in the vulnerability of forests to drought. *Nature*, 491, 752–755. <https://doi.org/10.1038/nature11688>
- Cornelissen, J. H. C. (1996). An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology*, 84, 573–582.
- Cornelissen, J. H. C., Cerabolini, B., Castro-Diez, P., Villar-Salvador, P., Montserrat-Marti, G., Puyravaud, J. P., Maestro, M., Werger, M. J. A., & Aerts, R. (2003). Functional traits of woody plants: Correspondence of species rankings between field adults and laboratory-grown seedlings? *Journal of Vegetation Science*, 14, 311–322.
- Cornelissen, J. H. C., Diez, P. C., & Hunt, R. (1996). Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology*, 84, 755–765.
- Cornelissen, J. H. C., Quested, H. M., Gwynn-Jones, D., Van Logtestijn, R. S. P., De Beus, M. A. H., Kondratyuk, A., Callaghan, T. V., & Aerts, R. (2004). Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Functional Ecology*, 18, 779–786.
- Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., van Bodegom, P., Brovkin, V., Chatain, A., ... Westoby, M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, 11, 1065–1071.
- Craven, D., Braden, D., Ashton, M. S., Berlyn, G. P., Wishnie, M., & Dent, D. (2007). Between and within-site comparisons of structural and physiological characteristics and foliar nutrient content of 14 tree species at a wet, fertile site and a dry, infertile site in Panama. *Forest Ecology and Management*, 238, 335–346.
- Dahlin, K. M., Asner, G. P., & Field, C. B. (2013). Environmental and community controls on plant canopy chemistry in a Mediterranean-type ecosystem. *Proceedings of the National Academy of Sciences USA*, 110(17), 6895–6900.

- Dang-Le, A. T., Edelin, C., & Le-Cong, K. (2013). Ontogenetic variations in leaf morphology of the tropical rain forest species *Dipterocarpus alatus* Roxb. *Ex G. Don. Trees*, 27, 773. <https://doi.org/10.1007/s00468-012-0832-2>
- De Frutos, Á., Navarro, T., Pueyo, Y., & Alados, C. L. (2015). Inferring resilience to fragmentation-induced changes in plant communities in a semi-arid Mediterranean ecosystem. *PLoS ONE*, 10, e0118837. <https://doi.org/10.1371/journal.pone.0118837>
- Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Martí, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. C., Shirvany, F. A., ... Zak, M. R. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, 15, 295–304.
- Domingues, T. F., Martinelli, L. A., & Ehleringer, J. R. (2007). Ecophysiological traits of plant functional groups in forest and pasture ecosystems from eastern Amazonia, Brazil. *Plant Ecology*, 193, 101–112. <https://doi.org/10.1007/s11258-006-9251-z>
- Domingues, T. F., Meir, P., Feldpausch, T. R., et al. (2010). Co-limitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands. *Plant, Cell & Environment*, 33, 959–980.
- Fagúndez, J., & Izco, J. (2008). Seed morphology of two distinct species of *Erica* L. (Ericaceae). *Acta Botanica Malacitana*, 33, 1–9.
- Fitter, A. H., & Peat, H. J. (1994). The ecological Flora database. *Journal of Ecology*, 82, 415–425.
- Fonseca, C. R., Overton, J. M., Collins, B., & Westoby, M. (2000). Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology*, 88, 964–977.
- Forgiarini, C., Souza, A. F., Longhi, S. J., & Oliveira, J. M. (2015). In the lack of extreme pioneers: Trait relationships and ecological strategies of 66 subtropical tree species. *Journal of Plant Ecology*, 8, 359–367. <https://doi.org/10.1093/jpe/rtu028>
- Freschet, G. T., Cornelissen, J. H. C., van Logtestijn, R. S. P., & Aerts, R. (2010). Evidence of the “plant economics spectrum” in a subarctic flora. *Journal of Ecology*, 98, 362–373.
- Fyllas, N. M., Patino, S., Baker, T. R., Bielefeld Nardoto, G., Martinelli, L. A., Quesada, C. A., Paiva, R., Schwarz, M., Horna, V., Mercado, L. M., Santos, A., Arroyo, L., Jimenez, E. M., Luizao, F. J., Neill, D. A., Silva, N., Prieto, A., Rudas, A., Silveira, M., ... Lloyd, J. (2009). Basin-wide variations in foliar properties of Amazonian forest: Phylogeny, soils and climate. *Biogeosciences*, 6, 2677–2708.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., ... Zarovali, M. P. (2007). Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, 99, 967–985.
- Giarrizzo, E., Burrascano, S., Chiti, T., de Bello, F., LepÁi, J., Zattero, L., & Blasi, C. (2016). Re-visiting historical semi-natural grasslands in the Apennines to assess patterns of changes in species composition and functional traits. *Applied Vegetation Science*. <https://doi.org/10.1111/avsc.12288>
- Gonzalez-Akre, E., McShea, W., Bourg, N., & Anderson-Teixeira, K. (2015). Leaf traits data (SLA) for 56 woody species at the Smithsonian Conservation Biology Institute-ForestGEO Forest dynamic plot. Front Royal, Virginia, USA [Data set]. Version 1.0. [www.try-db.org](http://www.try-db.org)
- Gos, P., Loucougaray, G., Colace, M. P., Arnoldi, C., Gaucherand, S., Dumazel, D., Girard, L., Delorme, S., & Lavorel, S. (2016). Relative contribution of soil, management and traits to co-variations of multiple ecosystem properties in grasslands. *Oecologia*, 180, 1001. <https://doi.org/10.1007/s00442-016-3551-3>
- Green, W. 2009. USDA PLANTS Compilation, version 1, 09-02-02. NRCS: The PLANTS Database (<http://plants.usda.gov>, 1 Feb 2009).
- National Plant Data Center: Baton Rouge, LA 70874–74,490 USA. <http://bricol.net/downloads/data/PLANTSdatabase/>
- Gutiérrez, A. G., & Huth, A. (2012). Successional stages of primary temperate rainforests of Chiloé Island, Chile. *Perspectives in Plant Ecology, Systematics and Evolution*, 14, 243–256.
- Hattermann, D., Elstner, C., Markus, B.-R., & Lutz, E. Measurements from the project “Relative effects of local and regional factors as drivers for plant community diversity, functional trait diversity and genetic structure of species on Baltic uplift islands” funded by the German Research Foundation—DFG: BE 4143/5–1 and EC 209/12–1.
- Hietz, P., Rosner, S., Hietz-Seifert, U., & Wright, S. J. (2017). Wood traits related to size and life history of trees in a Panamanian rainforest. *New Phytologist*, 213, 170–180.
- Higuchi, P., & Silva, A. C. (2013). Araucaria Forest Database.
- Jennifer, S. (2010). Powers and Peter tiffin 2012 plant functional type classifications in tropical dry forests in Costa Rica: Leaf habit versus taxonomic approaches. *Functional Ecology*, 24, 927–936. <https://doi.org/10.1111/j.1365-2435.2010.01701.x>
- Joseph, G. S., Seymour, C. L., Cumming, G. S., Cumming, D. H. M., & Mahlungu, Z. (2014). Termite mounds increase functional diversity of woody plants in African savannas. *Ecosystems*, 17, 808–819.
- Kattge, J., Knorr, W., Raddatz, T., & Wirth, C. (2009). Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology*, 15, 976–991.
- Kazakou, E., Vile, D., Shipley, B., Gallet, C., & Garnier, E. (2006). Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Functional Ecology*, 20, 21–30.
- Kichenin, E., Wardle, D. A., Peltzer, D. A., Morse, C. W., & Freschet, G. T. (2013). Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology*, 27(5), 1254–1261.
- Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J. M., Klimes, L., Klimesova, J., Klotz, S., Rusch, G. M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., ... Peco, B. (2008). The LEDA Traitbase: A database of life-history traits of the northwestern European flora. *Journal of Ecology*, 96, 1266–1274.
- Kraft, N. J. B., Valencia, R., & Ackerly, D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, 322, 580–582.
- Kühn, I., Durka, W., & Klotz, S. (2004). BioFlor—A new plant-trait database as a tool for plant invasion ecology. *Diversity and Distribution*, 10, 363–365.
- Kurokawa, H., & Nakashizuka, T. (2008). Leaf herbivory and decomposability in a Malaysian tropical rain forest. *Ecology*, 89, 2645–2656.
- Laughlin, D. C., Fulé, P. Z., Huffman, D. W., Crouse, J., & Laliberte, E. (2011). Climatic constraints on trait-based forest assembly. *Journal of Ecology*, 99, 1489–1499.
- Laughlin, D. C., Leppert, J. J., Moore, M. M., & Sieg, C. H. (2010). A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology*, 24, 493–501.
- Lhotsky, B., Anikó Csecserits, Bence Kovács, & Zoltán Botta-Dukát. New plant trait records of the Hungarian Flora.
- Li, R., Zhu, S., Chen, H. Y. H., John, R., Zhou, G., Zhang, D., Zhang, Q., & Ye, Q. (2015). Are functional traits a good predictor of global change impacts on tree species abundance dynamics in a subtropical forest? *Ecology Letters*, 18, 1181–1189. <https://doi.org/10.1111/ele.12497>
- Loveys, B. R., Atkinson, L. J., Sherlock, D. J., Roberts, R. L., Fitter, A. H., & Atkin, O. K. (2003). Thermal acclimation of leaf and root respiration: An investigation comparing inherently fast- and slow-growing plant species. *Global Change Biology*, 9, 895–910.
- Lukeš, P., Stenberg, P., Rautiainen, M., Möttus, M., & Vanhatalo, K. M. (2013). Optical properties of leaves and needles for boreal tree species in Europe. *Remote Sensing Letters*, 4(7), 667–676.

- Lusk, C. H., Kaneko, T., Grierson, E., & Clearwater, M. (2013). Correlates of tree species sorting along a temperature gradient in New Zealand rain forests: Seedling functional traits, growth and shade tolerance. *Journal of Ecology*, *101*, 1531–1541.
- Maire, V., Wright, I. J., Prentice, I. C., Batjes, N. H., Bhaskar, R., van Bodegom, P. M., Cornwell, W. K., Ellsworth, D., Niinemets, Ü., Ordoñez, A., Reich, P. B., & Santiago, L. S. (2015c). Data from: Global effects of soil and climate on leaf photosynthetic traits and rates. Dryad Digital Repository <https://doi.org/10.5061/dryad.j42m7>
- Maire, V., Wright, I. J., Prentice, I. C., Batjes, N. H., Bhaskar, R., van Bodegom, P. M., Cornwell, W. K., Ellsworth, D., Niinemets, Ü., Ordoñez, A., Reich, P. B., & Santiago, L. S. (2015b). Global soil and climate effects on leaf photosynthetic traits and rates. *Global Ecology and Biogeography*, *24*(6), 706–717.
- Martinez-Garza, C., Bongers, F., & Poorter, L. (2013a). Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? *Forest Ecology and Management*, *303*, 35–45.
- Medlyn, B. E., Badeck, F.-W., De Pury, D. G. G., Barton, C. V. M., Broadmeadow, M., Ceulemans, R., De Angelis, P., Forstreuter, M., Jach, M. E., Kellomäki, S., Laitat, E., Marek, M., Philippot, S., Rey, A., Strassmeyer, J., Laitinen, K., Liozon, R., Portier, B., Robertz, P., ... Jarvis, P. G. (1999). Effects of elevated CO<sub>2</sub> on photosynthesis in European forest species: A meta-analysis of model parameters. *Plant, Cell and Environment*, *22*, 1475–1495.
- Meir, P., Kruijt, B., Broadmeadow, M., Kull, O., Carswell, F., & Nobre, A. (2002). Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf nitrogen concentration and leaf mass per unit area. *Plant, Cell and Environment*, *25*(3), 343–357. 15 p.
- Meir, P., & Levy, P. E. (2007). Photosynthetic parameters from two contrasting woody vegetation types in West Africa. *Plant Ecology*, *192*(2), 277–287. 11 p.
- Messier, J., McGill, B. J., & Lechowicz, M. J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, *13*, 838–848.
- Michaletz, S. T., & Johnson, E. A. (2006). A heat transfer model of crown scorch in forest fires. *Canadian Journal of Forest Research*, *36*(11), 2839–2851.
- Milla, R., & Reich, P. B. (2011). Multi-trait interactions, not phylogeny, fine-tune leaf size reduction with increasing altitude. *Annals of Botany*, *107*, 455–465.
- Moretti, M., & Legg, C. (2009). Combining plant and animal traits to assess community functional responses to disturbance. *Ecography*, *32*, 299309. <https://doi.org/10.1111/j.1600-0587.2008.05524.x>
- Mori, A. S., Shiono, T., Haraguchi, T. F., Ota, A. T., Koide, D., Ohgue, T., Kitagawa, R., Maeshiro, R., Aung, T. T., Nakamori, T., Hagiwara, Y., Matsuoka, S., Ikeda, A., Hishi, T., Hobara, S., Mizumachi, E., Frisch, A., Thor, G., Fujii, S., ... Gustafsson, L. (2015). Functional redundancy of multiple forest taxa along an elevational gradient: Predicting the consequences of non-random species loss. *Journal of Biogeography*, *42*, 1383–1396. <https://doi.org/10.1111/jbi.12514>
- Niinemets, U. (2001). Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology*, *82*, 453–469.
- Ogaya, R., & Penuelas, J. (2003). Comparative field study of *Quercus ilex* and *Phillyrea latifolia*: Photosynthetic response to experimental drought conditions. *Environmental and Experimental Botany*, *50*, 137–148.
- Onstein, R. E., Carter, R. J., Yaowu Xing, H., & LinderInstitute, P. (2014). Diversification rate shifts in the cape floristic region: The right traits in the right place at the right time. *Perspectives in Plant Ecology, Evolution and Systematics*, *16*(6), 331–340. <https://doi.org/10.1016/j.ppees.2014.08.002>
- Ordóñez, J. C., van Bodegom, P. M., Witte, J. P. M., Bartholomeus, R. P., van Hal, J. R., & Aerts, R. (2010). Plant strategies in relation to resource supply in Mesic to wet environments: Does theory Mirror nature? *American Naturalist*, *175*, 225–239.
- Paula, S., Arianoutsou, M., Kazanis, D., Tavsanoğlu, Ç., Lloret, F., Buhk, C., Ojeda, F., Luna, B., Moreno, J. M., Rodrigo, A., Espelta, J. M., Palacio, S., Fernández-Santos, B., Fernandes, P. M., & Pausas, J. G. (2009). Fire-related traits for plant species of the Mediterranean Basin. *Ecology*, *90*, 1420.
- Penuelas, J., Sardans, J., Llusia, J., Owen, S., Carnicer, J., Giambelluca, T. W., Rezende, E. L., Waite, M., & Niinemets, Ü. (2010). Faster returns on “leaf economics” and different biogeochemical niche in invasive compared with native plant species. *Global Change Biology*, *16*, 2171–2185.
- Pierce, S., Brusa, G., Vagge, I., & Cerabolini, B. E. L. (2013). Allocating CSR plant functional types: The use of leaf economics and size traits to classify woody and herbaceous vascular plants. *Functional Ecology*, *27*(4), 1002–1010.
- Pillar, V. D., & Sosinski, E. E. (2003). An improved method for searching plant functional types by numerical analysis. *Journal of Vegetation Science*, *14*, 323–332.
- Poorter, H., Niinemets, U., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist*, *182*, 565–588.
- Prentice, I. C., Meng, T., Wang, H., Harrison, S. P., Ni, J., & Wang, G. (2011). Evidence for a universal scaling relationship of leaf CO<sub>2</sub> drawdown along a moisture gradient. *New Phytologist*, *190*, 169–180.
- Preston, K. A., Cornwell, W. K., & DeNoyer, J. L. (2006). Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytologist*, *170*, 807–818.
- Price, C. A., & Enquist, B. J. (2007). Scaling of mass and morphology in dicotyledonous leaves: An extension of the WBE model. *Ecology*, *88*(5), 1132–1141.
- Quested, H. M., Cornelissen, J. H. C., Press, M. C., Callaghan, T. V., Aerts, R., Trosien, F., Riemann, P., Gwynn-Jones, D., Kondratyuk, A., & Jonasson, S. E. (2003). Decomposition of sub-arctic plants with differing nitrogen economies: A functional role for hemiparasites. *Ecology*, *84*, 3209–3221.
- Reich, P. B., Oleksyn, J., & Wright, I. J. (2009). Leaf phosphorus influences the photosynthesis-nitrogen relation: A cross-biome analysis of 314 species. *Oecologia*, *160*, 207–212.
- Reich, P. B., Tjoelker, M. G., Pregitzer, K. S., Wright, I. J., Oleksyn, J., & Machado, J. L. (2008). Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. *Ecology Letters*, *11*, 793–801.
- Royal Botanical Gardens KEW. 2008. Seed Information Database (SID). Version 7.1. Available from: <http://data.kew.org/sid/> (May 2011).
- Royal Botanical Gardens KEW Seed Information Database (SID). <http://data.kew.org/sid/>
- Scherer-Lorenzen, M., Schulze, E.-D., Don, A., Schumacher, J., & Weller, E. (2007). Exploring the functional significance of forest diversity: A new long-term experiment with temperate tree species (BIOTREE). *Perspectives in Plant Ecology, Evolution and Systematics*, *9*, 53–70.
- Shiodera, S., Rahajoe, J. S., & Kohyama, T. (2008). Variation in longevity and traits of leaves among co-occurring understorey plants in a tropical montane forest. *Journal of Tropical Ecology*, *24*, 121–133.
- Shpley, B. (2002). Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: Relationship with daily irradiance. *Functional Ecology*, *16*(5), 682–689.
- Shpley, B., & Vu, T. T. (2002). Dry matter content as a measure of dry matter concentration in plants and their parts. *New Phytologist*, *153*, 359–364.
- Siefert, A. (2012). Spatial patterns of functional divergence in old-field plant communities. *Oikos*, *121*, 907–914.
- Slot, M., Rey-Sanchez, C., Winter, K., & Kitajima, K. (2014). Trait-based scaling of temperature-dependent foliar respiration in a species-rich tropical forest canopy. *Functional Ecology*, *28*, 1074–1086. <https://doi.org/10.1111/1365-2435.12263>
- Swaine, E. K. (2007). *Ecological and evolutionary drivers of plant community assembly in a Bornean rain forest*. PhD thesis. University of Aberdeen.

- Takkis, K. (2014). Changes in plant species richness and population performance in response to habitat loss and fragmentation. *Dissertationes Biologicae Universitatis Tartuensis* 255, 2014-04-07 <http://hdl.handle.net/10062/39546>
- van de Weg, M. J., Grace, P. M. J., & Ramos, G. D. (2011). Photosynthetic parameters, dark respiration and leaf traits in the canopy of a Peruvian tropical montane cloud forest. *Oecologia*. <https://doi.org/10.1007/s00442-011-2068-z>
- van de Weg, M. J., Meir, P., Grace, J., & Atkin, O. (2009). Altitudinal variation in leaf mass per unit area, leaf tissue density and foliar nitrogen and phosphorus content along the Amazon-Andes gradient in Peru. *Plant Ecology & Diversity*, 2(3), 243–254.
- van der Plas, F., & Olf, H. (2014). Mesoherbivores affect grasshopper communities in a megaherbivore-dominated South African savannah. *Oecologia*, 175, 639. <https://doi.org/10.1007/s00442-014-2920-z>
- Vergutz, L., S. Manzoni, A. Porporato, R.F. Novais, and R.B. Jackson. 2012. *A global database of carbon and nutrient concentrations of Green and senesced leaves* [Data set]. Oak Ridge National Laboratory Distributed Active Archive Center. <http://daac.ornl.gov>. <https://doi.org/10.3334/ORNLDAAC/1106>
- Vile, D. 2005. *Significations fonctionnelle et ecologique des traits des especes vegetales: exemple dans une succession post-cultural mediterraneenne et generalisations*. [Doctoral thesis, Université de Sherbrook.]
- Walker, A.P. 2014. *A global data set of leaf photosynthetic rates, leaf N and P, and specific leaf area*. [Data set]. Oak Ridge National Laboratory Distributed Active Archive Center. <http://daac.ornl.gov>. <https://doi.org/10.3334/ORNLDAAC/1224>
- Willis, C. G., Halina, M., Lehman, C., Reich, P. B., Keen, A., McCarthy, S., & Cavender-Bares, J. (2010). Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. *Ecography*, 33, 565–577.
- Wilson, K. B., Baldocchi, D. D., & Hanson, P. J. (2000). Spatial and seasonal variability of photosynthetic parameters and their relationship to leaf nitrogen in a deciduous forest. *Tree Physiology*, 20(9), 565–578.
- Wirth, C., & Lichstein, J. W. (2009). The imprint of species turnover on old-growth Forest carbon balances - insights from a trait-based model of Forest dynamics. In C. Wirth, G. Gleixner, & M. Heimann (Eds.), *Old-growth forests: Function, fate and value* (pp. 81–113). Springer.
- Wright, I. J., Ackerly, D. D., Bongers, F., Harms, K. E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Paz, H., Pitman, N. C. A., Poorter, L., Silman, M. R., Vriesendorp, C. F., Webb, C. O., Westoby, M., & Wright, S. J. (2007). Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Annals of Botany*, 99, 1003–1015.
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.
- Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E., Condit, R., Dalling, J. W., Davies, S. J., Díaz, S., Engelbrecht, B. M. J., Harms, K. E., Hubbell, S. P., Marks, C. O., Ruiz-Jaen, M. C., Salvador, C. M., & Zanne, A. E. (2011). Functional traits and the growth-mortality tradeoff in tropical trees. *Ecology*, 91, 3664–3674.
- Xu, L. K., & Baldocchi, D. D. (2003). Seasonal trends in photosynthetic parameters and stomatal conductance of blue oak (*Quercus douglasii*) under prolonged summer drought and high temperature. *Tree Physiology*, 23, 865–877.