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Spatial patterns and climate relationships of major plant traits in the New World differ between woody and herbaceous species

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Abstract

Aim: Despite several recent efforts to map plant traits and to identify their climatic drivers, there are still major gaps. Global trait patterns for major functional groups, in particular, the differences between woody and herbaceous plants, have yet to be identified. Here, we take advantage of big data efforts to compile plant species

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occurrence and trait data to analyse the spatial patterns of assemblage means and variances of key plant traits. We tested whether these patterns and their climatic drivers are similar for woody and herbaceous plants.

Location: New World (North and South America).

Methods: Using the largest currently available database of plant occurrences, we provide maps of 200 × 200 km grid-cell trait means and variances for both woody and herbaceous species and identify environmental drivers related to these patterns. We focus on six plant traits: maximum plant height, specific leaf area, seed mass, wood density, leaf nitrogen concentration and leaf phosphorus concentration.

Results: For woody assemblages, we found a strong climate signal for both means and variances of most of the studied traits, consistent with strong environmental filtering. In contrast, for herbaceous assemblages, spatial patterns of trait means and variances were more variable, the climate signal on trait means was often different and weaker.

Main conclusion: Trait variations for woody versus herbaceous assemblages appear to reflect alternative strategies and differing environmental constraints. Given that most large-scale trait studies are based on woody species, the strikingly different biogeographic patterns of herbaceous traits suggest that a more synthetic framework is needed that addresses how suites of traits within and across broad functional groups respond to climate.

KEYWORDS

BIEN database, environmental filtering, functional biogeography, growth form, habit, macroecology, plant functional traits, plant functional types, TRY database

1 | INTRODUCTION

The geography of plant functions is unequivocally a foundation of plant ecology (e.g. Schimper, 1898). Just as the functional characterization of species has reinvigorated the field of community ecology (McGill, Enquist, Weiher, & Westoby, 2006), the functional characterization of assemblages at large spatial scales is likely to provide novel insights about the drivers of biogeographic patterns in species diversity and ecosystem functioning (Lamanna et al., 2014; Stahl, Reu, & Wirth, 2014). Such developments reflect the shift from a "biogeography by taxa" to a "biogeography by functions" (Chown & Gaston, 2008, 2016; Chown, Gaston, & Robinson, 2004; Gaston et al., 2009; Reichstein, Bahn, Mahecha, Kattge, & Baldocchi, 2014; Swenson et al., 2012; Violle, Reich, Pacala, Enquist, & Kattge, 2014).

Numerous studies have assessed spatial gradients in plant traits in relation to the environment (e.g. Chave et al., 2009; Moles et al., 2009; Swenson et al., 2012; Wright et al., 2004, 2005). However, a general set of patterns has yet to emerge, which challenges the assumption of universal and predictable trait–environment relationships (Shipley et al., 2016). Trait–environment correlations are often weak (e.g. $r^2 < .3$ in Moles et al., 2014) and the strength and sign of these correlations can vary across studies. For example, in some studies plant height has been reported to increase most strongly with precipitation (Moles et al., 2009; Šímová et al., 2015; Swenson et al., 2012), whereas others have reported the strongest relationship with mean annual temperature (Moles et al., 2014). In some studies leaf nitrogen concentration increased with decreasing temperature (Moles et al., 2014; Šímová, Rueda, & Hawkins, 2017; Wright et al., 2005), whereas in others leaf nitrogen concentration showed the opposite pattern (Ordoñez et al., 2009; Swenson et al., 2012); it has also been found to be most strongly related to precipitation (Swenson & Weiser, 2010). Results concerning trait variances diverge even more across studies (Šímová et al., 2015, 2017; Swenson & Weiser, 2010; Swenson et al., 2012). These inconsistencies could be due to various factors such as differences in sampling scale, sparsity of data, methods of inference, historical legacies, sensitivity to land use and the specific growth forms studied (Borgy, Violle, Choler, Denelle et al., 2017; Borgy, Violle, Choler, Garnier et al., 2017). Many studies have combined woody and herbaceous species in single analyses (e.g. Moles et al., 2014), which may have obscured divergent trait–climate relationships. Using traits related to the stature of plants, Díaz et al. (2016) have shown that herbaceous and woody species form two almost independent hotspots in the global spectrum of plant form and function, indicating the fundamental difference between these two groups. Differences between these two groups in their functional adaptations to environmental conditions have also been identified (Ordoñez et al., 2010; Petit & Hampe, 2006; Reich, Ellsworth, & Walters, 1998; Ricklefs & Latham, 1992). We therefore propose that these two basic growth form strategies —herbaceous versus woody plants—should be analysed separately to better identify and understand fundamental trait–climate relationships.

Here, we focus on the geographic patterns of plant functional traits across North and South America and ask: What are the spatial patterns of means and variances in trait values of woody and herbaceous assemblages and how do these patterns differ between growth forms? Which environmental drivers are related to these patterns, and do they have similar effects on both woody and herbaceous plants? We take advantage of two plant databases: (1) the BIEN database of species' traits, occurrences and range maps covering the entire New World (Botanical Information and Ecology Network; Enquist, Condit, Peet, Schildhauer, & Thiers, 2016; Maitner et al., in press), and (2) the TRY Plant Trait Database (www.try-db.org; Kattge et al., 2011). We use two types of species distribution data: species occurrences and species range maps. Both types of data have advantages and disadvantages. Species occurrences data document presence with high certainty, but are biased by uneven sampling intensity, resulting in numerous gaps due to false absences. Species range maps are much less affected by sampling bias and false absences, but as they are modelled in part using climate variables, their use can introduce circularity into analyses of trait–climate correlations. We therefore restricted our analyses to occurrence data only and used species range maps to verify the occurrence-based spatial trait patterns. We examined the following plant traits related to key plant ecological strategies (Díaz et al., 2016): plant height, specific leaf area (SLA) and seed mass as representatives of major plant strategies (Westoby, 1998), and leaf nitrogen and phosphorus concentrations per mass as key resource use–related traits (Chown & Gaston, 2008). For trees, we also included wood density, a key trait in the wood economics spectrum (Chave et al., 2009).

2 | MATERIALS AND METHODS

2.1 | Species distribution data

The BIEN (Botanical Information and Ecology Network) database (http://bien.nceas.ucsb.edu/bien/biendata/bien-3/) integrates 20,465,306 plant observations that have been standardized for taxonomy and georeferences and that have their coordinates within North or South America. Observations stem from herbarium specimens and vegetation plot inventories. The BIEN 3.0 dataset (retrieved on 13 November 2014) consists of 114,412 plant species in the continental New World (see Appendix 1 for the reference list). Most of these data are now publicly available via the "BIEN" R package (Maitner et al., in press) with some exceptions concerning the coordinates of endangered species and records from private databases (see Maitner et al., in press for details).

As an additional species distribution dataset, we used the BIEN 2.0 range maps available for 88,417 New World species (Goldsmith et al., 2016). The method of building the range maps differed depending on the number of occurrences per species available in the database: A species with only one or two occurrence records was assigned a fixed range of 75,000 km^2 surrounding each occurrence point. Species with 3–4 records had their ranges defined as convex hulls. Ranges for species with >5 records were modelled using the MAXENT species distribution modelling algorithm with a balanced set of climate predictors and spatial eigenvectors (Phillips, Anderson, & Schapire, 2006; see Goldsmith et al., 2016, for details on the range maps methodology).

We overlaid the BIEN 3.0 occurrences on a 200 × 200 km grid (Lambert Azimuthal Equal Area projection) to obtain a species list for each grid cell. We repeated the same procedure with the species' range maps of BIEN 2.0. We chose this resolution as it is robust to potential overestimation of area of occupancy by individual species derived from range maps (Hurlbert & Jetz, 2007). We only included cells with more than 80% of their area on land.

2.2 | Trait data

We analysed variation in six functional traits: maximum plant height (m), SLA (cm^2/g), seed mass (mg), leaf phosphorus and leaf nitrogen concentration per mass (Leaf N and Leaf P) (mg/g), and wood density (mg/cm^3). We combined the BIEN and TRY trait data (retrieved on 19 October 2014; a list of the data sources is found in Appendix 1). Merging TRY and BIEN resulted in the largest plant trait compilation for North and South America to date, including more than 70,000 species-level observations for the six plant traits used in the study.

Growth form data were taken from Engemann et al. (2016). Species with more than one growth form assignment were included only if >2/3 of the observations of a given species agreed on one growth form (see Engemann et al., 2016 for details). We split the species data into two functional groups: "woody" and "herbaceous". We considered plants scored as tree, shrub or liana as "woody", whereas "herbaceous" plants were represented by those scored as herbs, grasses, ferns, vines and epiphytes. We excluded mosses and aquatic species. We were able to assign a growth form to 47,784 species having georeferenced occurrence records (21,390 woody and 26,394 herbaceous species). Among these, we obtained 6,107 woody and 6,056 herbaceous species with at least one known trait value (Appendix S1). The best coverage was for seed mass (3,060 woody and 5,259 herbaceous species), whereas the lowest coverage was for leaf P (1,754 woody and 808 herbaceous species) (see Figures S2.1 and S2.2 and Table S2.1 for details on trait coverage).

Prior to analyses, we $\log_e$ transformed the values of seed mass, height and wood density to correct for skewness in trait distributions and to improve the normality of the residuals in the fitted statistical models. In addition, we checked for outlying trait values and manually removed unrealistic outliers assumed to be probable errors in trait observations (10 values total).

2.3 | Environmental data

We included six climatic predictors (representing 1960–1990 conditions) that have been commonly used in trait-based studies and/or represent different aspects of climate affecting plant ecophysiology (e.g. Lambers, Chapin, & Pons, 2008; Larcher, 2003). Mean annual temperature (°C), annual precipitation sum (mm), temperature seasonality (standard deviation of monthly temperature multiplied by 100) and precipitation seasonality (coefficient of variation of monthly precipitation) were taken from the WorldClim database (version 1.4; www.worldclim.org, Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Mean annual solar radiation was obtained from CliMond (accessed 7 July 2015; https://www.climond.org/BioclimData.aspx; Kriticos et al., 2012). Global aridity index was obtained from CGIAR-CSI GeoPortal (accessed 21 April 2014; http://www.cgiar-csi.org/; Trabucco & Zomer, 2010). This index is calculated as the ratio of annual precipitation to potential evapotranspiration, with higher values of this index representing lower aridity. We projected the climate variables to the Lambert Azimuthal Equal Area projection using nearest-neighbour interpolation and resampled each variable to 200 × 200 km grid size by computing mean values for each grid cell using the R "raster" package (Hijmans et al., 2016; R Development Core Team, 2017).

2.4 | Data analyses

We first coupled the species occurrences from each grid cell to the species-level trait data. We separated woody and herbaceous species (except for wood density, which only applies to woody species). Next, using species' trait values per grid cell, we calculated per-cell mean and variance for each trait and repeated this calculation using the species occurrences inferred from the range maps. We separately mapped trait patterns based on species occurrences and on occurrences inferred from the range maps. Trait maps based on species occurrences per grid cell can be spatially biased because of differential sampling intensity and the presence of species with extreme trait values (Borgy, Violle, Choler, Garnier et al., 2017). To address this, we excluded grid cells with a higher variance than the 99% quantile for the respective traits (Figure S2.3) and two grid cells of extremely high values of mean leaf N and SLA.

We used spatial correlations to compare the similarity in geographical patterns of both woody and herbaceous trait means and variances based on species occurrences versus species occurrences inferred from the range maps. We used the Pearson correlation coefficient and Dutilleul's method of correction for degrees of freedom to account for spatial autocorrelation (package "SpatialPack"; Osorio & Vallejos, 2014).

Next, we searched for climatic predictors of trait means and variances using model selection according to the Akaike information criteria (AIC) weight (Burnham & Anderson, 2002; Wagenmakers & Farrell, 2004). We used the *dredge* function in the R "MuMIn" package (Barton, 2016). As the trait–climate relationship can be nonlinear, we used all six climate variables in their linear and quadratic form (12 explanatory variables in total). To reduce the model complexity and identify the most important predictors, we limited the number of terms in the model output to a maximum of six (results presented in the main text). In addition, we also performed a model with unlimited number of the output terms (results presented in Appendix S3). Researchers have argued that AIC approach tends to select overly complex models (e.g. Kass & Raftery, 1995). Therefore, to verify our results, we additionally performed a Lasso model selection; results presented in Appendix S3.

To compare woody and herbaceous trait–climate relationships, we re-ran the model selection for the combined dataset of standardized trait means (or variances) for both growth forms together. Standardization was done by dividing the centred variables by their standard deviations (function *scale* in R; Becker, Chambers, & Wilks, 1988). As explanatory variables, we included (1) the subset of standardized climate variables selected in the model selection process explained above, (2) the interaction terms between all these climate variables (in their linear forms) and the growth form (woody or herbaceous), and (3) the growth form (woody or herbaceous). Similarly, as above, we limited the number of terms in the model output to a maximum of six and we additionally performed the selection with unlimited number of terms in the model output and the Lasso model selection (Zhao & Yu, 2006; results presented in Appendix S3).

In addition, we examined separate linear regression models for each climate variable with the combined dataset of standardized trait means (or variances) for both growth form groups together as response variables and standardized climate (in its linear and quadratic form), the growth form–climate interaction term and the main effect of growth form as explanatory variables. Specifically, we tested for the significance of the interaction term between climate and growth form. When the trait–climate relationship is the same for both woody and herbaceous species, we expect a significant climate signal, but a non-significant effect of the interaction term.

The availability of species trait values is likely to vary geographically, which could bias the results. Therefore, we weighted the regression models by the square root of the per-cell number of species with known values of a particular trait (the results presented in the main text), and compared the results with unweighted regression models (results presented in Appendix S3).

3 | RESULTS

3.1 | Comparison of trait patterns based on occurrences to patterns based on range maps

Variation in most trait patterns based on species occurrences per grid cell corresponded well to variation in trait patterns based on species occurrences inferred from species range maps (Table 1). The closest match between the two methods was for all trait means of woody species, whereas the weakest match was for means and variances of leaf N and leaf P of herbaceous species and for variance in wood density of woody species. The spatial patterns were generally stronger for woody species compared to herbaceous species.

3.2 | Climate signals on trait means and variances in woody and herbaceous species

We found strong trait–climate relationships for trait means of woody species (Table 2, average r^2 = .67), but much weaker relationships for herbaceous trait means (Table 2, average r^2 = .22) and for most woody and herbaceous trait variances (Table 2, average r^2 = .38 for woody and .33 for herbaceous species).

Mean height of woody species primarily increased with mean annual temperature, with the tallest trees occurring above 10°C (Figure S3.6). Although mean height of herbaceous species also increased with increasing temperature, its best predictor was solar radiation, with the tallest species at sites of medium radiation (Figure S3.6). Mean SLA of woody species increased with increasing temperature and precipitation, although these relationships became flatter after reaching 10°C and 1500 mm, respectively (Figure S3.6). Woody SLA also increased curvilinearly with increasing temperature seasonality. Herbaceous mean SLA primarily increased with increasing temperature and precipitation, similar to woody SLA. Woody seed mass strongly increased with increasing precipitation. Mean seed mass of both growth form groups also increased with mean annual temperature, although this relationship was much weaker for herbaceous species. Mean leaf N of woody species increased with increasing temperature and decreasing solar radiation. Although temperature was also the best predictor of herbaceous leaf N, the relationship was much weaker. Mean leaf P of woody species was higher but variable outside the tropics and uniformly lower within the tropics (Figure 1, column 1), and its variation strongly correlated with temperature seasonality. Little spatial pattern was evident for herbaceous mean leaf P (Figure 1, column 2), consistent with the weak sensitivity to environmental variables (model r^2 = .05). Mean wood density increased with increasing temperature and decreasing precipitation. These results remained qualitatively similar when performing a model selection with unlimited number of terms in the model output (Table S3.2) and when performing a Lasso model selection (Table S3.3), except that in the latter case, the importance of the solar radiation was rather weak.

TABLE 1 Pearson correlation coefficients (*r*) between trait means (means) or variances (vars) based on species occurrences and those based on species ranges maps. "W" is woody habit, "H" is herbaceous habit. *Indicates significant correlation ($p < .05$) and (*) indicates marginally significant correlation ($p < .1$) when accounting for the effect of space using Duttieul's method

Trait	Habit	*r* (means)	*r* (vars)
Height	W	.844*	.604*
Height	H	.552*	.605
SLA	W	.695*	.473*
SLA	H	.413*	.315(*)
Seed mass	W	.891*	.470*
Seed mass	H	.186*	.281*
Leaf N	W	.708*	.571*
Leaf N	H	.237*	.282(*)
Leaf P	W	.768*	.285*
Leaf P	H	−.003	.244*
Wood density	W	.762*	.055

In contrast to the high correlations between climate and trait means (for woody species assemblages), correlations between climate and most trait variances were weaker (average r^2 = .36; Table 2). Trait variances were often predicted by solar radiation (woody height, SLA, herbaceous seed mass, woody leaf N and leaf P) and temperature seasonality (herbaceous height, herbaceous leaf P), but the form of these relationships was variable (Table 2, Figures S3.9–S3.11). For instance, whereas variance in height of herbaceous species decreased curvilinearly with increasing temperature seasonality, this relationship was nearly unimodal for variance in woody SLA and height. Similarly, whereas variance in height, herbaceous SLA, and woody leaf P increased with decreasing solar radiation, the relationship was opposite for herbaceous seed mass and woody SLA. These results were qualitatively similar when performing a model selection with unlimited number of terms in the model output (Table S3.2). Nevertheless, when using a Lasso model selection, the results were frequently different and solar radiation remained a strong and important predictor of variance in herbaceous SLA only (Table S3.3).

When testing for the similarity in trait–climate relationships between the growth forms using model selection with standardized variables, the growth form–climate interaction term was a relatively strong and important predictor of almost all trait means and variances (Table 3). This indicates that each growth form displays a different relationship with particular climate variables (Figure 2). The variable with the strongest impact on the dissimilarity in trait–climate relationship between the growth forms was often temperature seasonality. The results largely remained the same when performing a model selection with unlimited number of terms in the model output and when performing a Lasso model selection (Tables S3.5–S3.6). Here, both mean annual temperature and temperature seasonality often had the strongest impact on the difference between woody and herbaceous species. When testing for the effect of the growth form–climate interaction terms using separate linear regression models for each climate variable, the effect of the growth form–climate interaction term was significant in most cases, further supporting the different responses of woody and herbaceous trait means and variances to climate (Figures S3.12–S3.17).

Most of the observed relationships between trait means and climate remained when performing a model selection based on the unweighted regression (Table 2 vs. Table S3.4). The only differences occurred for poorly sampled traits such as herbaceous leaf N and leaf P. However, for trait variances, the results based on the unweighted regression were frequently different from the weighted results. Like for the weighted models, the unweighted trait–climate relationships for standardized variables differed between woody and herbaceous species (Tables 3 vs. S3.7). Nevertheless, the variable having the strongest impact on the difference between woody and herbaceous species was often mean annual temperature rather than temperature seasonality. The effect of the interaction term of climate and the growth form on trait means was weaker, however, when compared to the results based on the weighted regression. Higher noise in the data of poorly sampled regions (e.g. Amazon

TABLE 2 The best models explaining trait means and variances of each trait selected according to AIC weight. Coefficients below each explanatory variable have been standardized and indicate the relative contribution of this variable to each model. The number of terms in the model output is limited to a maximum of six. See Table S3.2 for the results for an unlimited number of terms and Table S3.3 for Lasso model selection. "W" is woody habit, "H" is herbaceous habit, "T" is mean annual temperature, "P" is annual precipitation, "TS" is temperature seasonality, "PS" is precipitation seasonality, "Arid" is aridity index (P/PET) and "Solar" is annual solar radiation. Each variable is represented by the linear form (e.g. T) and quadratic form (e.g. T^2). See Figures S3.6–S3.11 for plots of the respective contribution of each predictor. All these models were weighted by square root of the per-cell number of species with known trait. See Table S3.4 for the unweighted models

Trait	Habit	r^2	T	T^2	P	P^2	TS	TS^2	PS	PS^2	Arid	$Arid^2$	Solar	$Solar^2$
Mean														
Height	W	.82	1.27	−0.77	0.33		−0.99	1.07				−0.11		
Height	H	.39	0.91	−0.49		0.13		0.38					1.42	−1.43
SLA	W	.42	1.53	−1.15	1.20	−0.80	−0.50	1.05						
SLA	H	.36	0.88	−0.71	0.40			0.19				−0.06	−0.30	
Seed mass	W	.86	0.77	−0.28	1.03	−0.37		0.15			−0.30			
Seed mass	H	.18	0.63	−0.43				0.16					0.40	−0.43
Leaf N	W	.52	0.90	−0.41			−0.21				−0.15		−1.17	1.08
Leaf N	H	.13	0.23	−0.38				−0.21			−0.11			−0.12
Leaf P	W	.83	0.70	−0.69	0.10		1.43	−0.75			−0.17			
Leaf P	H	.05	0.22	−0.26			−0.11							−0.14
Wood density	W	.60	0.97	−0.15	−0.16				−0.19	0.19				
Variance														
Height	W	.65	−0.33			−0.20	0.90	−0.89					−1.17	1.00
Height	H	.56				−0.09	−1.53	0.92		−0.06			−1.23	1.25
SLA	W	.19		−0.17			0.52	−0.52	0.15				1.54	−1.32
SLA	H	.32	0.82	−0.67		0.13		0.30					−2.61	2.14
Seed mass	W	.46		−0.30	1.20	−0.62	−0.38		−0.13			−0.20		
Seed mass	H	.26		0.19				0.12			0.37	−0.16	0.82	−0.81
Leaf N	W	.44		−0.18				−0.65		−0.18			−1.13	1.16
Leaf N	H	.16			0.54	−0.26	−0.24				−0.51	0.17		−0.21
Leaf P	W	.28	1.12	−1.23					−0.36	0.41			−2.38	2.41
Leaf P	H	.35				−0.15	−1.14	0.65						0.06
Wood density	W	.22		−0.29					0.09		−0.45	0.36		

basin) can thus partly mask the differences in trait–climate relationships between growth forms.

4 | DISCUSSION

By using the largest and most complete large-scale plant distribution and trait datasets for the New World, we found strong spatial patterns and climatic associations for several key plant functional traits. Consistent with existing evidence and theoretical expectations (Kerkhoff, Enquist, Elser, & Fagan, 2005; Moles & Westoby, 2003; Reich, 2014), we found that compared to colder environments, warmer and wetter environments are characterized by taller plants with larger seeds and leaves characterised by greater area per unit biomass. However, trait–climate relationships differed overall between woody and herbaceous species, including different climate predictors or different shapes of the trait–climate relationships.

Means and variances of herbaceous traits appeared less strongly linked to climate than woody traits. These differences were strongest for mean leaf phosphorus concentration, seed mass and variance in height and specific leaf area. Such discrepancies may result from the higher diversity in strategies among herbaceous species when compared to woody species. This corresponds to existing evidence that herbaceous species tend to occupy smaller, more specialized niches than woody species (Ricklefs & Latham, 1992). There are several possible explanations for the weaker climate signal for herbaceous species. In particular, the microclimate perceived by understorey herbaceous communities is not captured by macroclimate variables (Schneider et al., 2004). Interestingly, the variable with the strongest impact on the dissimilarity in trait–climate relationship between the two growth forms was often temperature seasonality. Differences in strategies to cope with unfavourable seasons thus seem to be the key factor responsible for the difference in woody versus herbaceous trait values.

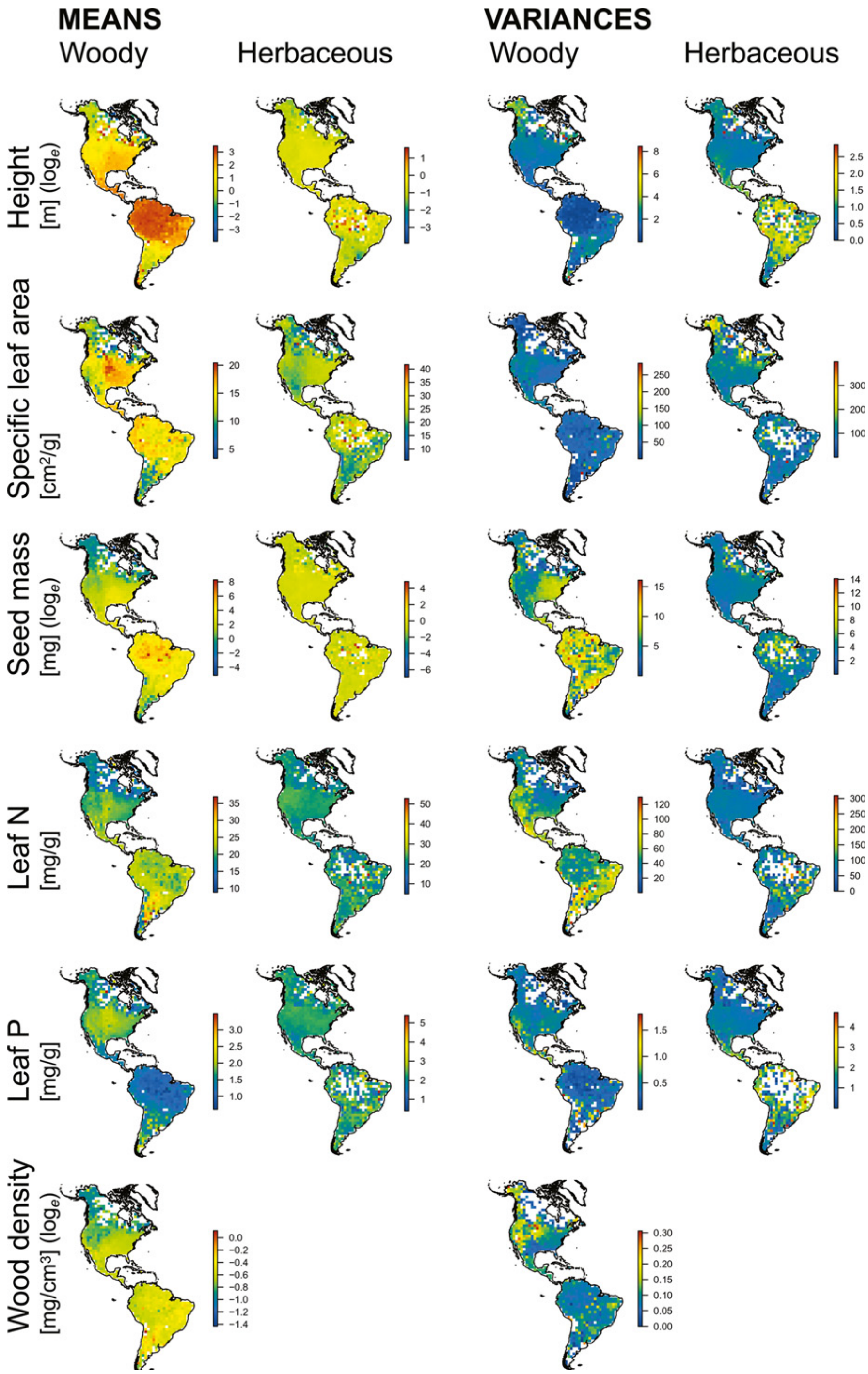

FIGURE 1 Trait maps of grid-cell trait means and variances for woody species (the first and third columns) and herbaceous species (the second and fourth columns). Note that trait values of height, seed mass and wood density were log$_e$-transformed prior calculating grid-cell trait means and variances. See Figures S2.4 and S2.5 for comparison to trait maps based on species ranges maps

Our findings that some trait–climate relationships depend on growth form have important implications for studies predicting the functional response of ecosystems to changing climate. Although numerous large-scale studies focus on woody species only and make strong generalizations from this growth form, our results imply that plant woodiness must be considered to adequately assess the importance of climate for plant traits. Importantly, the differences between growth forms may explain the weak trait–climate relationships observed in previous studies that pooled all growth forms for analysis (e.g. Moles et al., 2014; Ordoñez et al., 2009).

Consistent with expectations of strong and predictable trait–environment relationships (Lavorel & Garnier, 2002; Shipley et al., 2016), variation in plant traits showed significant correlations with climate variables. Mean annual temperature, temperature seasonality and solar radiation were among the best predictors of these traits, which is in line with the species-level approach of Moles et al. (2014). Seasonality of precipitation had, in turn, the lowest effects on trait means and variances, suggesting that it plays a less important role in the biogeography of these traits at continental scales. Many of the observed trait–climate correlations are broadly

TABLE 3 The best models explaining trait means and variances merged for both growth form groups selected according to the AIC weight. Coefficients below each explanatory variable are standardized and indicate the relative contribution of this variable to each model. The number of terms in the model output is limited to a maximum of six. See Table S3.5 for the results for an unlimited number of terms and Table S3.6 for Lasso model selection output. See Table 2 for explanations of abbreviations of environmental variables. "GF" is growth form (woody/herbaceous). Each variable is represented by the linear term (e.g. T), quadratic term (e.g. T^2) and interaction term with growth form (e.g. GF:T). Note that precipitation seasonality was omitted as it was not selected in any case. All variables were standardized prior analysis. All models were weighted by square root of the per-cell number of species with known trait. See Table S3.7 for the unweighted models

Trait	r^2	T	T^2	P	P^2	TS	TS^2	Arid	$Arid^2$	Solar	$Solar^2$	GF	GF: T	GF:P	GF:TS	GF: Arid	GF: Solar
Mean																	
Height	.61	0.42		0.14		0.43					−0.23	−0.01			−0.41		
SLA	.54		−0.48	0.98	−0.41	0.86						0.02			−0.48		
Seed mass	.56	0.35	−0.39				0.22				−0.20	−0.11			−0.40		
Leaf N	.59	−0.55	−0.16			−0.70				0.27		−0.08	0.36				
Leaf P	.76					−0.36	−0.04				−0.12	0.15			1.11		0.21
Variance																	
Height	.54	−0.17				−0.76					0.14	0.09		−0.17	0.74		
SLA	.40					0.56				−0.31	−0.09	0.17			−0.27		0.51
Seed mass	.51		−0.33			−0.41	0.24	0.48	−0.24			−0.10					
Leaf N	.51		−0.21			−0.61		−0.15			0.26	0.05				−0.17	
Leaf P	.43					−0.48				−0.07	0.19	0.09			0.91		0.36

consistent with existing hypotheses and past studies focused on single trait–climate correlations. Murray et al. (2004) hypothesized that warmer environments increase metabolic rates, leading to the higher metabolic costs for seedlings and, thus, a need for larger seeds, whereas Moles and Westoby (2003) hypothesized that larger seeds would be favoured under warm and wet conditions due to higher competitive pressures. Consistent with these predictions, mean seed mass increases with increasing temperature (results also found in Moles et al., 2009; Šímová et al., 2015; Swenson & Weiser, 2010) and precipitation. Similarly, consistent with Ryan and Yoder's (1997) hydraulic limitation hypothesis for trees, mean height increases towards warm and wet climates as hydraulic pathways are increasingly vulnerable to frost and drought embolisms (Ryan & Yoder, 1997; Stegen et al., 2011). The observed increase in wood density with increased temperature is also consistent with the hydraulic limitation hypothesis as denser wood in warmer, drought-prone environments provides increased mechanical support in the form of resistance to xylem conduit implosion or rupture (Hacke, Sperry, Pockman, Davis, & McCulloh, 2001). Consistent with Kerkhoff et al. (2005), leaf phosphorus concentration of woody species tends to increase, whereas leaf nitrogen concentration tends to decrease in colder, more seasonal environments. Kerkhoff et al. (2005) argued that such environments would select for increased phosphorus concentration relative to nitrogen concentration to increase growth rates and growth efficiencies. It is also possible that lower leaf phosphorus in tropical plant tissues results from lower soil phosphorus concentration in tropical ecosystems (Quesada et al., 2009). The mean specific leaf area of both woody and herbaceous species decreases with decreasing temperature and with decreasing precipitation (consistent with empirical findings of Hulshof et al., 2013; Šímová et al., 2015; Swenson et al., 2012). This corresponds to the trade-off between slow photosynthetic rate and long leaf lifespan under stressful conditions versus fast tissue turnover and high potential for resource capture under more favourable conditions (Reich, 2014). It is also consistent with a recent hypothesis that lower specific leaf area in colder environments helps modulate leaf temperatures (Michaletz et al., 2016). Interestingly, specific leaf area of both growth form groups increased with increasing temperature seasonality after accounting for the effect of temperature and precipitation. A possible explanation is that some species (e.g. winter deciduous trees) require higher photosynthetic rates to adapt to a short growing season.

Other observed trait correlations with climate are not consistent with any existing hypotheses and do not have any precedent in the literature. For example, in contrast to previous reports of inconsistent relationships between leaf nitrogen concentration and climate (Moles et al., 2014; Ordoñez et al., 2009; Swenson et al., 2012), temperature and solar radiation were both strong predictors of woody leaf nitrogen concentration in our study. This may reflect an increased frequency of nitrogen-fixing trees towards lower latitudes, producing a shift in nitrogen use strategy (Menge, Lichstein, & Ángeles-Pérez, 2014).

Furthermore, in contrast to some previous studies and expectations, we found little evidence that harsh environments reduce the number of viable strategies (e.g. Swenson et al., 2012). Overall, the variation in trait variances along environmental gradients was often rather weak. This is consistent with recent findings indicating that the environment affects large-scale assemblage composition by

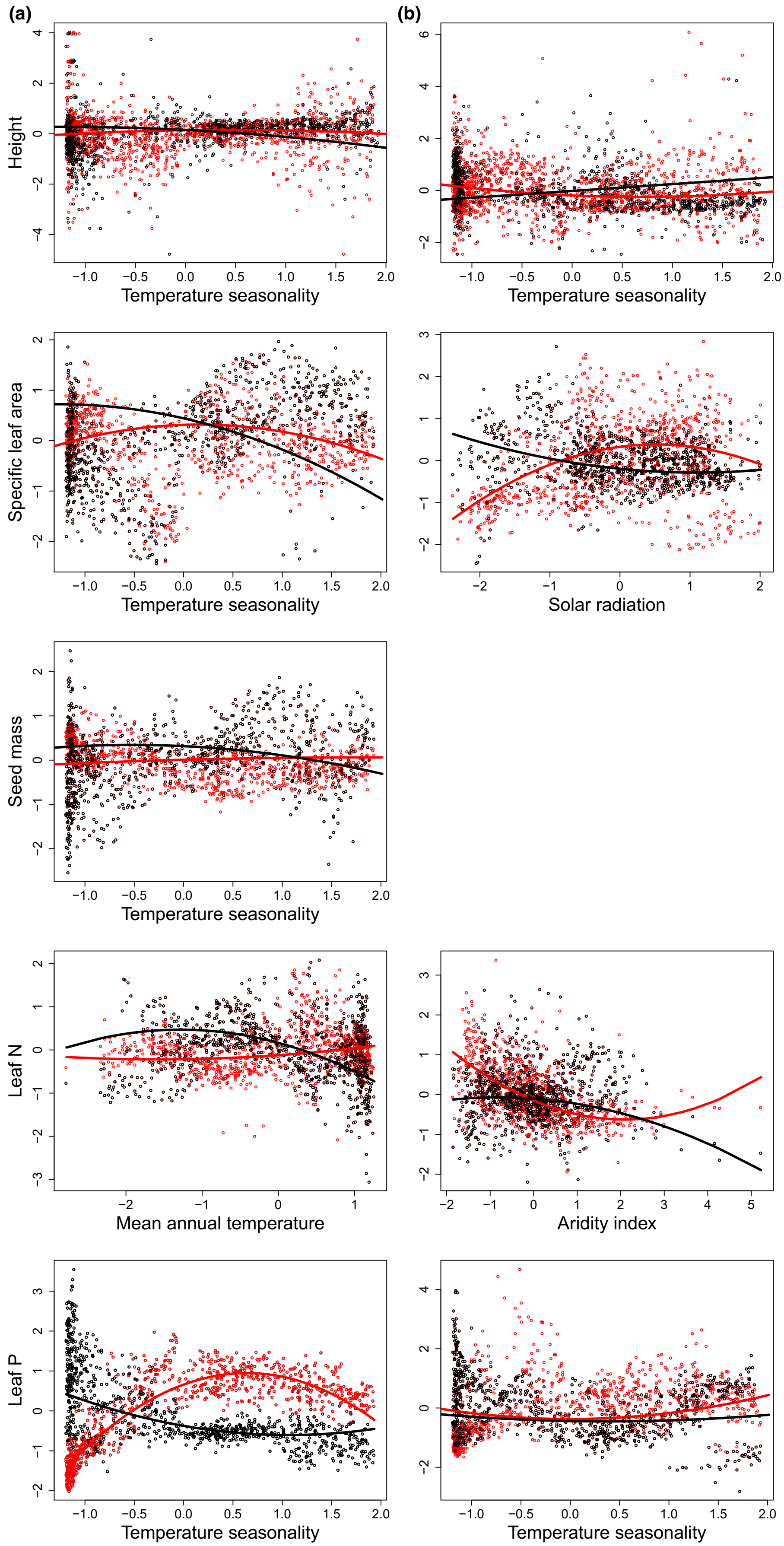

FIGURE 2 The relationships of partial effect of standardized (a) trait means and (b) variances for woody species (red circles) and herbaceous species (black circles) plotted against the standardized climatic predictor having the strongest impact on the difference between the growth forms (Table 3). For variance in seed mass, none of the growth form–climate interaction terms was selected. The variable on the *y*-axis is calculated as residuals of the linear regression model with standardized trait means (a) and variances (b) for both growth forms together as a response variable and its climate predictors presented in Table 3 (without the variable on the *x*-axis) as explanatory variables. Note that woody and herbaceous trait means and variances were standardized separately. The model fit is a quadratic regression

selecting for a certain optimal trait values rather than constraining trait variances (Šímová et al., 2015, 2017). It is also possible that trait divergence is more driven by biotic interactions (even if debatable at the grid size under scrutiny, see Damgaard & Weiner, 2017) or environmental heterogeneity not captured in our analyses. Nevertheless, given that the results concerning trait variances were highly sensitive to different model selection approaches, they should be interpreted with caution.

Interestingly, the spatial patterns of traits were largely similar when the underlying data were species occurrences or species occurrences as inferred from species range maps. Species distribution models have improved significantly in recent years (Merow et al., 2014; Thuiller, Lavorel, Sykes, & Araújo, 2006; Thuiller, Munkemuller, Moller, Fiedler, & Berthold, 2010) and range maps are increasingly available for many plant species worldwide. These advances will facilitate large-scale studies focused on functional traits. An important next step for quantifying spatial variation in traits is to predict changes in ecosystem services (Violle, Choler, et al., 2015) or vegetation dynamics at large spatial scales under global climate change scenarios (Scheiter, Langan, & Higgins, 2013). However, caution must be used in interpreting some results. For instance, merging leaf nitrogen or phosphorus concentration values with range maps of herbaceous species in under-sampled regions of South America generated strong spatial patterns (Figure S2.4, column 4), but the ecological meaning of such patterns remains unclear. On the other hand, at high latitudes (such as Canada in the case of this study), where species ranges are large and the vegetation is relatively homogenous, species range maps can improve maps of plant functional traits. The estimation of errors and uncertainties when using incomplete and heterogeneous datasets thus remains a priority for assessing the credibility of findings in the emerging field of functional biogeography (Borgy, Violle, Choler, Garnier et al., 2017; Violle, Borgy, & Choler, 2015).

Even though our results are based on the best plant trait and species distribution data currently available at this extensive spatial scale, they must be viewed in light of several important caveats. First, we used only mean species trait values and ignored intra-specific trait variability. Although some traits show greater plasticity than others (Kattge et al., 2011; Kazakou et al., 2014), intra-specific trait variation may be more important to incorporate when exploring species assembly processes at smaller scales than at larger scales that cover multiple and strongly heterogeneous biomes (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011; Siefert et al., 2015; Violle et al., 2012) and exceed the range limits for most of the component species. Second, our measures of trait means and variances are not weighted by the relative abundance of those species within each grid cell. As a result, rare species are given as much statistical weight as common species. We suspect that accounting for trait abundance by using weighted measures of trait means and variances would strengthen the relationships (Borgy, Violle, Choler, Denelle et al., 2017). Third, our analyses are based on a relatively coarse spatial resolution. Although this resolution should be robust to potential overestimation of species distributions derived from range maps (Hurlbert & Jetz, 2007), finer resolution should better capture local environmental conditions and could lead to stronger trait–climate relationships. A more important issue, however, is spatial sampling bias. A substantial fraction of the tropical species, especially the South American species, is lacking trait values. We showed that, whereas trait means were relatively robust to the spatial unevenness of species occurrence records, trait variances were much more sensitive to sampling bias and their relationships to climate should thus be interpreted with caution. Fortunately, the number of trait measurements in large databases continues to increase. Furthermore, our maps of sampling intensity (Figures S2.1 and S2.2) can guide ecologists and plant physiologists to where future field measurements of trait values are needed.

Our results have important implications for the emerging field of functional biogeography. First, observed relationships between trait means and variances are helping to assess several prominent hypotheses regarding the climate signal on plant traits (e.g. the hydraulic limitation hypothesis, the seed mass-environmental favourability hypothesis). Second, the differences in trait–climate correlations observed for woody versus herbaceous species imply that it is critical to differentiate between woody and herbaceous plants in large-scale, trait-based studies. An important next step for future studies will be to combine the maps of trait means and variances with maps of ecosystem processes (e.g. remotely sensed productivity data). This will enable us to evaluate the relative importance of both in driving ecosystem processes, a long-standing goal of functional ecology (Díaz et al., 2007; Enquist et al., 2015; Lavorel, 2013). In turn, this will help refine structure and simulation of dynamic vegetation models over large spatial scales (Reichstein et al., 2014) and improve predictions of ecosystem services (Violle, Choler, et al., 2015).

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DATA ACCESSIBILITY

All raster maps in asci format, species occurrence—grid data table, list of the taxa used in our analyses and main data frame are available in online Supporting Information (Appendix S1). Species coordinates are available via "BIEN" R package with some exceptions of endangered species (see Maitner et al., in press for details). Trait data are available via BIEN (http://bien.nceas.ucsb.edu/bien/biendata/bien-3/) and TRY (www.try-db.org).

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BIOSKETCH

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Author contributions: C.V., I.S., B.J.E. and J.C.-S. conceived the study; I.S. analysed the data with help from A.T. and P.v.B.; I.S. and C.V. led the writing with major contributions from J.C.-S., K.E., R.K.P., J.K., B.S., B.B., S.K.W. and B.J.E.; B.J.E., B.B., R.K.P., J.-C.S., S.K.W., C.V., N.J.B.K., N.M.-H. and B.J.M. developed the BIEN database (http://bien.nceas.ucsb.edu/bien/), J.K. provided the TRY database, and P.M.v.B., A.G.G., M.B. and W.A.O. were core TRY contributors. All authors discussed and commented on the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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APPENDIX 1

DATA SOURCES

ORIGINAL DATA SOURCES FOR SPECIES OCCURRENCE DATA EXTRACTED FROM THE BIEN DATABASE

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