



RESEARCH
PAPER

The biogeography and filtering of woody plant functional diversity in North and South America

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ABSTRACT

Aim In recent years evidence has accumulated that plant species are differentially sorted from regional assemblages into local assemblages along local-scale environmental gradients on the basis of their function and abiotic filtering. The favourability hypothesis in biogeography proposes that in climatically difficult regions abiotic filtering should produce a regional assemblage that is less functionally diverse than that expected given the species richness and the global pool of traits. Thus it seems likely that differential filtering of plant traits along local-scale gradients may scale up to explain the distribution, diversity and filtering of plant traits in regional-scale assemblages across continents. The present work aims to address this prediction.

Location North and South America.

Methods We combine a dataset comprising over 5.5 million georeferenced plant occurrence records with several large plant functional trait databases in order to: (1) quantify how several critical traits associated with plant performance and ecology vary across environmental gradients; and (2) provide the first test of whether the woody plants found within 1° and 5° map grid cells are more or less functionally diverse than expected, given their species richness, across broad gradients.

Results The results show that, for many of the traits studied, the overall distribution of functional traits in tropical regions often exceeds the expectations of random sampling given the species richness. Conversely, temperate regions often had narrower functional trait distributions than their smaller species pools would suggest.

Main conclusion The results show that the overall distribution of function does increase towards the equator, but the functional diversity within regional-scale tropical assemblages is higher than that expected given their species richness. These results are consistent with the hypothesis that abiotic filtering constrains the overall distribution of function in temperate assemblages, but tropical assemblages are not as tightly constrained.

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INTRODUCTION

Global patterns of plant species richness have been a focus of biogeographers for well over a century (Wallace, 1878; Schimper, 1898). Recent studies have produced remarkably detailed maps depicting how plant species richness varies across the earth (Kier *et al.*, 2005; Mutke & Barthlott, 2005), fostering more thorough tests of the numerous hypotheses put forward to explain the origin and maintenance of species diversity (e.g. Currie *et al.*, 2004; Weiser *et al.*, 2007). Despite our increased ability to map and analyse plant species diversity, similar maps and analyses of alternative axes of biodiversity, such as functional diversity, have lagged behind (Swenson & Weiser, 2010; Swenson, 2011). This is problematic, as it is organismal function and not species names that interact with, and evolve in response to, the environment. Thus it will be difficult to test mechanistic hypotheses regarding the geographic distribution of biodiversity without a consideration of the distribution of organismal function (Swenson, 2011).

Plant ecologists frequently consider the critical role of species function in determining the observed distribution of diversity in local plant assemblages (e.g. Tilman *et al.*, 1997; Weiher *et al.*, 1998). A common thread in much of this research has been the potential linkage between the observed functional diversity in assemblages and the degree of abiotic filtering along an environmental gradient within a study location (Weiher *et al.*, 1998). In particular, abiotic filtering is expected to constrain the overall distribution of function observed within assemblages, with the greatest amount of filtering occurring in the least favourable locations along a local-scale gradient. Many have extended this approach to consider a counter-gradient where biotic interactions become more important in more favourable abiotic conditions, thereby giving rise to a reduction in functional similarity between species within a local assemblage (e.g. Weiher & Keddy, 1995). Combined, this suggests that the overall distribution of functional diversity and the functional similarity of individual species in local assemblages should vary predictably along local environmental gradients. As species richness also varies along these same gradients, tests of these predictions generally require the usage of null models that control for the coincidental gradient in species richness and ask whether the observed distribution of functional diversity in an assemblage is any different from that expected by a random sampling of some species pool.

Scaling up analyses that compare a few local-scale assemblages within a region to comparing the assemblages of entire regions across continents has been a key limitation to our understanding of the functional underpinnings of biodiversity gradients (Swenson & Enquist, 2007). Interestingly, classic

discussions of the latitudinal gradient in species richness have invoked mechanisms similar to those used to describe the assembly and diversity of plant communities on local scales. In particular, the favourability hypothesis in biogeography highlights the potential importance of increased abiotic filtering from the tropics to the temperate zone (Fischer, 1960). Conversely in relatively more climatically benign climates a broader diversity of forms may be able to exist.

While it is almost certain that no single mechanism will explain the distribution of species and functional diversity across local- or broad-scale gradients, there is substantial evidence that gradients in abiotic filtering may explain a great deal of the local-scale spatial variation in functional diversity in plant communities (e.g. Weiher *et al.*, 1998; Stubbs & Wilson, 2004; Cornwell *et al.*, 2006; Kraft *et al.*, 2008; Swenson & Enquist, 2009; Swenson *et al.*, 2011). Less well explored or established is whether the favourability hypothesis can be supported on larger spatial scales, with evidence that plant functional diversity is non-randomly filtered along broad gradients. In particular, a general decrease in functional diversity with latitude is expected given the coincidental decrease in species richness, but stronger abiotic filtering in the temperate zone should cause temperate zone assemblages to have a lower than expected functional diversity given their observed species richness. Thus it may be possible that the mechanism of increasingly strong abiotic filtering along environmental gradients may govern not only the distribution and diversity of functional traits in local-scale plant assemblages but also in regional-scale assemblages.

Here we provide the first broad-scale test of this prediction using a large and novel combined dataset for six key plant traits [leaf %N, leaf %P, specific leaf area (SLA; leaf area divided by dry leaf mass), seed mass, maximum height and wood density] that are indicative of species positions along major axes of ecological strategy variations (Westoby, 1998; Westoby *et al.*, 2002). This functional trait dataset was joined to a database of over 5.5 million georeferenced woody plant occurrence records from the New World, allowing us to map species functional trait values into grid cells throughout the western hemisphere based on the assemblage of species found within each grid cell. We then generated maps of two different components of functional diversity using three different metrics. The functional diversity metric, FD (Petchey & Gaston, 2002), and the mean pair-wise functional trait distance (PW) both provide measures of the overall dispersion of trait values for each local assemblage. In contrast, the mean nearest neighbour functional trait distance (NN) provides an average dissimilarity measure that describes how the species are 'packed' into the functional trait 'space'. These observed levels of functional trait diversity were then compared to that expected given the observed species richness and the global trait

pool using null models in order to determine whether the observed level of functional trait diversity was higher or lower than that randomly expected.

METHODS

Functional trait selection

The plant traits chosen for this study have been shown to be robust indicators of where a species falls along a few key dimensions of plant functional variation (Westoby, 1998; Westoby *et al.*, 2002). We acknowledge that a number of other plant traits, such as plant defence and hydraulic traits, are of interest, but due to data limitations they were not included in the present study. Foliar %N and %P and SLA are key traits in the 'leaf economics spectrum' (Reich *et al.*, 1997; Wright *et al.*, 2004). The leaf economics spectrum represents where a species falls along a continuum of strategies ranging from high structural investment, long leaf life span and low nutrient content versus low structural investment, short leaf life span and high nutrient content. Seed mass indicates where a species lies along the spectrum of species producing many small seeds or few large seeds per unit energy (Venable, 1996; Moles & Westoby, 2006). Maximum height indicates the adult light niche of a species (Kohyama, 1993; Moles *et al.*, 2009). Wood density is correlated with growth and mortality rates and represents a trade-off between mechanical strength and vertical growth (Swenson & Enquist, 2007; Chave *et al.*, 2009).

Plant functional trait geographic information system

Our plant trait database consisted of trait values from existing databases [plant height: USDA Plants Database (USDA, 2006); seed mass: Kew Millennium Seed Database (Moles *et al.*, 2005; Flynn *et al.*, 2008); SLA: Glopnet (Reich *et al.*, 1997; Wright *et al.*, 2004), wood density (Swenson & Enquist, 2007; Chave *et al.*, 2009); leaf %N and %P (Wright *et al.*, 2004; Kerkhoff *et al.*, 2006)]. This core database was supplemented with large data sets field collected by a subset of the authors in Costa Rica, Puerto Rico (Swenson *et al.*, 2007; Swenson & Enquist, 2008, 2009; Uriarte *et al.*, 2010; Swenson *et al.*, 2011) and Ecuador (Kraft *et al.*, 2008) and by compiling trait values from the published literature. The literature search aimed to locate articles reporting trait values for large numbers of woody species (> 30), but no formal search utilizing citation databases was done. A list of the literature used to supplement the core trait database is provided in Table S1 and Appendix S1 in the Supporting Information. Taxonomic delineations followed the International Plant Names Index (<http://www.ipni.org>); standardization was achieved using TaxonScrubber (<http://www.salvias.net/pages/taxonscrubber.html>). The distributional database SALVIAS (<http://www.salvias.net>; Weiser *et al.*, 2007) currently holds c. 4.2 million individual georeferenced plant occurrences taken from herbarium specimens and forest inventory plots spanning the globe. Major data contributors to the SALVIAS data portal include the Missouri Botanical Garden via Tropicos, REMIB, the

University of Arizona Herbarium, the University of British Columbia Herbarium, and the University of Tennessee Herbarium. As the SALVIAS database has poor geographic coverage for Brazil, it was merged with independent georeferenced specimens stored in the online database CRIA (<http://www.cria.org.br>). The CRIA database is a compilation of herbarium records for several regional and national herbaria in Brazil and Colombia. A full listing of these herbaria is available on the CRIA web portal. The United States Forest Inventory and Analysis (FIA) dataset (<http://fia.fs.fed.us>) was added to the SALVIAS and CRIA datasets to enhance the North American coverage. When combined, these three databases constituted more than 5.5 million georeferenced records of plant occurrence. As with the trait database, TaxonScrubber was also used to standardize taxonomy in the species occurrence database. Each record in this combined occurrence database was geographically binned into 1° and 5° grid cells. As many ecological patterns are scale dependent, we conducted all analyses reported here at both spatial scales. Analyses of local-scale patterns across both continents were not feasible and we therefore limit our inferences to hypotheses regarding regional- or biogeographic-scale processes. We present the results of the 1° grid cell analyses in the main text and the results of the 5° grid cell analyses in Appendix S1.

Next, the list of unique species names for each grid cell was extracted. This list was joined to the trait databases where the mean trait value for a given species was assigned. The resulting specimen × trait matrix table was imported into GIS software as a vector point file and then converted into one raster grid map at the resolution of 1° for each trait and one map at the resolution of 5° for each trait. These maps depict the mean functional trait value inside each grid cell.

Functional diversity analyses

To calculate the functional trait diversity in each map grid cell we generated functional trait dendrograms for each trait. Prior to dendrogram construction all maximum height, seed mass and SLA data were log₁₀-transformed. The dendrograms, constructed using hierarchical clustering (Petchey & Gaston, 2002), considered only the species found in both the functional trait dataset and the plant occurrence databases. Figures of the dendrograms are available in Appendix S1. Using the functional trait dendrograms we calculated three metrics of functional trait diversity. The first was the functional diversity metric, FD (Petchey & Gaston, 2002), which calculates the shared dendrogram branch lengths found in a grid cell represented as a proportion of the total possible dendrogram branch lengths. The second metric was the mean pair-wise trait distance, PW, between all species within a grid cell. This is a functional trait dendrogram analogue of the MPD phylogenetic metric of Webb (Webb, 2000). The FD and PW metrics are similar (Mouchet *et al.*, 2010), but the values generated by these metrics do not necessarily represent redundant information. For example, the FD metric is highly correlated with species richness, whereas the PW metric is largely independent of the species richness of an

Table 1 Spearman rank correlations between the mean trait value in a map grid cell and physiographic and climatic variables.

Trait	Lat	Alt	MAT	TS	TR	AP	PS
Maximum height	0.25	−0.05	−0.10	0.15	0.16	0.16	−0.25
Leaf %N	−0.01	0.18	0.23	−0.04	−0.05	0.14	0.23
Leaf %P	0.62	0.07	−0.54	0.65	0.62	−0.42	0.30
Seed mass	−0.26	−0.20	0.47	−0.43	−0.44	0.50	0.01
Specific leaf area	−0.48	−0.19	0.33	−0.40	−0.36	0.44	0.07
Wood density	−0.61	−0.24	0.62	−0.54	−0.51	0.23	0.33

Lat, absolute value of latitude; Alt, altitude; MAT, mean annual temperature; TS, temperature seasonality (standard deviation of 12 mean monthly temperatures); TR, annual temperature range (maximum – minimum annual temperatures); AP, total annual precipitation; PS, precipitation seasonality (coefficient of variation of 12 monthly rainfall totals). Bold values indicate significant correlations ($P < 0.05$).

assemblage. The third metric was the mean nearest-neighbour trait distance, NN, between species within a grid cell. This is a functional trait dendrogram analogue of the MNND phylogenetic metric of Webb (Webb, 2000).

Next, we used a null model approach to determine whether the observed cell-specific FD, PW and NN values were greater or less than expected given the observed, cell-specific species richness. Specifically 9999 random assemblages were generated for each trait and for each grid cell. This was done by randomizing the names of taxa across the tips of the dendrograms 9999 times and recalculating each metric during each iteration. This procedure keeps all observed spatial patterns such as dispersal limitation, contagion of species distributions, species occupancy rates and grid cell species richness constant while only randomizing the trait dataset.

The observed FD, PW and NN values for each grid cell and for each trait were then compared with the null distributions to calculate the quantile in which they fell and to calculate a standardized effect size (SES). The SES was calculated as the observed value minus the mean of the null distribution divided by the standard deviation of the null distribution. This randomization procedure makes the assumption that through evolutionary time all global trait values could have invaded every region or evolve *in situ*. All randomizations were written and executed using the statistical software R.

We calculated Spearman rank correlations of the mean trait value, the three functional trait diversity metrics, the functional trait diversity standardized effect sizes with species richness, and the absolute value of latitude, altitude and climatic variables. Climate data were derived from a 30'' gridded dataset consisting of interpolated 50-year normals from New World weather stations (Hijmans *et al.*, 2005). The results from the trait analyses and the independent variables used in the correlative analyses had a high degree of spatial autocorrelation such that the degrees of freedom calculated from the number of map grid cells was an overestimate. We took account of this spatial autocorrelation within the climatic and trait data using the 'Clifford' method implemented in the software SAM (Rangel *et al.*, 2006); this software calculates the appropriate degrees of freedom given the observed non-independence in the data.

Functional diversity sensitivity analyses

As the woody plant occurrence and trait databases utilized in this study are heterogeneous in their coverage, we performed a series of sensitivity analyses designed to determine whether or not the results and inferences reported are robust. Specifically, we assessed potential biases due both to spatial heterogeneity in database coverage and to the undersampling of incompletely described (principally tropical) woody floras. We addressed spatial heterogeneity in two ways. First we performed all of the analyses again at the resolution of 5° map grid cells in order to minimize artefacts due to small-scale spatial heterogeneity. Second, we performed a rarefaction analysis in which we randomly sampled, without replacement, 25 species in each map grid cell (both 1° and 5°) that had sufficient trait data. This was repeated 100 times for each map grid cell and mean SES FD, SES PW and SES NN metrics were calculated for each trait.

Potential biases due to sampling only common species in the databases were estimated using tropical forest inventory plots that have comprehensive trait databases. In each inventory plot, we quantified the SES FD, SES PW and SES NN for only the top 5% of the most common species. This value was compared with values calculated using assemblages that included increasingly rare species, until the entire forest plot species list was included.

There are several sensitivity analyses regarding potential biases in the trait and occurrence datasets that could not be performed due to a lack of information available. For example it is possible that there is a latitudinal bias in the lumping versus splitting of species that could influence the degree of functional similarity in assemblages across latitude, but there is no strong quantitative evidence of this that could be incorporated into a sensitivity analyses. A second bias could be due to trait variation within species ranges, but substantial datasets documenting these patterns are not available.

RESULTS

Distribution of plant function

In general, the mean functional trait value in map grid cells varied with climate and latitude (Table 1 and Fig. 1). Leaf %P,

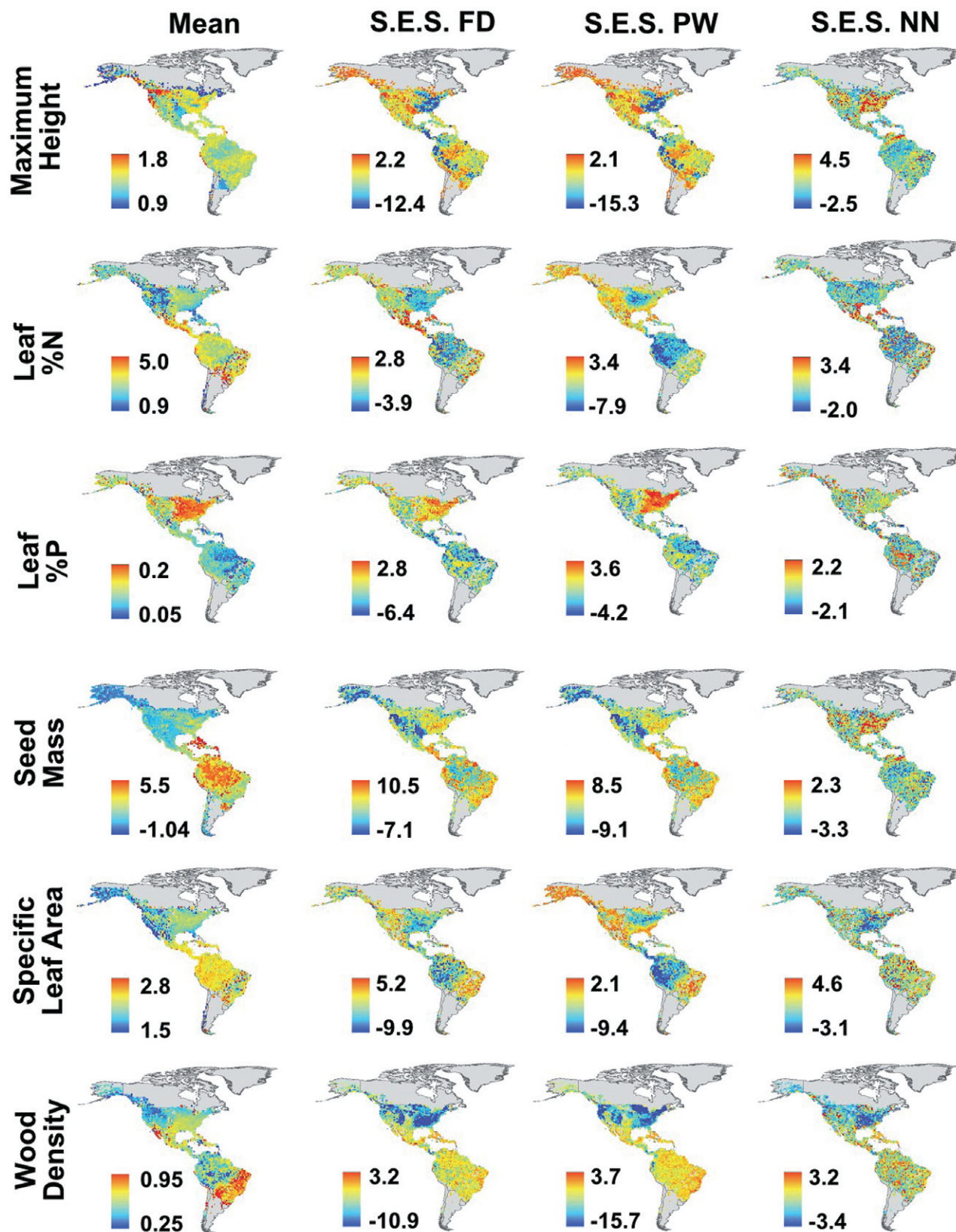


Figure 1 The geographic distribution and diversity of plant function in North and South America. The first column represents the mean trait value in each grid cell with warm colours indicating high trait values and cool colours indicating low trait values (SES, standardized effect size). The second, third, and fourth columns represent the functional trait diversity (FD), the mean pairwise trait distance (PW) and the mean nearest trait neighbour distance (NN) values, respectively, with warm colours indicating high functional trait diversity and cool colours indicating low functional trait diversity.

Table 2 Spearman Rank correlations between the dispersion of trait values in a map grid cell and physiographic and climatic variables.

Trait	Metric	Latitude	Altitude	MAT	TS	TR	AP	PS
Maximum height	SES FD	-0.132	-0.153	0.249	-0.189	-0.202	0.273	-0.099
	SES PW	-0.127	-0.152	0.242	-0.181	-0.194	0.273	-0.113
	SES NN	0.133	-0.018	0.094	-0.163	-0.172	0.125	0.114
Leaf % N	SES FD	0.107	-0.160	0.062	0.011	-0.006	0.213	0.242
	SES PW	-0.431	-0.271	0.463	-0.417	-0.437	0.572	0.106
	SES NN	0.062	-0.016	-0.103	0.124	0.123	0.001	0.124
Leaf % P	SES FD	0.428	-0.039	-0.398	-0.465	-0.462	0.322	0.238
	SES PW	0.347	0.045	-0.313	-0.422	-0.404	0.230	0.295
	SES NN	0.097	-0.035	-0.103	-0.075	-0.079	0.044	0.046
Seed mass	SES FD	-0.350	-0.131	0.342	-0.310	-0.311	0.254	0.049
	SES PW	-0.366	-0.125	0.344	-0.246	-0.274	0.221	0.010
	SES NN	0.131	-0.002	0.089	-0.153	-0.160	0.114	0.092
Specific leaf area	SES FD	-0.121	-0.149	0.107	-0.052	-0.083	0.236	0.232
	SES PW	-0.262	-0.166	0.362	-0.336	-0.353	0.499	0.174
	SES NN	-0.154	-0.043	-0.121	0.178	0.164	-0.088	0.118
Wood density	SES FD	-0.543	-0.112	0.546	-0.619	-0.602	0.274	0.438
	SES PW	-0.565	-0.135	0.587	-0.629	-0.612	0.288	0.418
	SES NN	-0.374	-0.071	0.367	-0.413	-0.400	0.214	0.187

SES, standardized effect size; FD, functional diversity; PW, mean pair-wise functional trait distance; NN, nearest functional neighbour distance; Lat, absolute value of latitude; Alt, altitude; MAT, mean annual temperature; TS, temperature seasonality (standard deviation of 12 mean monthly temperatures); TR, annual temperature range (maximum – minimum annual temperatures); AP, total annual precipitation; PS, precipitation seasonality (coefficient of variation of 12 monthly rainfall totals). Bold values indicate significant correlations ($P < 0.05$).

wood density, seed mass and SLA were strongly correlated with latitude and/or climate, while leaf %N and maximum height showed weaker, or non-significant, correlations with climatic gradients. In particular tropical assemblages tend to have higher seed size, wood density and SLA values, on average, than their temperate counterparts. Many of these results are consistent with previous findings (e.g. Reich & Oleksyn, 2004; Kerkhoff *et al.*, 2005; Moles *et al.*, 2007; Swenson & Enquist, 2007; Chave *et al.*, 2009; Elser *et al.*, 2010), suggesting that the results produced in this work derived using inherently heterogeneous sampling can still recover established climate–trait relationships.

Diversity of plant function

The null modelling analyses indicate that for four of the six traits, functional diversity of woody plant species is actually even greater than that expected given the species richness in tropical latitudes when using the SES FD and SES PW metrics (Table 2 and Figs 1 & 2). Leaf %N and leaf %P were the two exceptions to this, with higher than expected diversity in temperate latitudes. This temperate–tropical contrast was especially strong for SLA and wood density, which had greater functional dispersion in warm, aseasonal, tropical environments. While the SES PW metric generally seemed more strongly correlated with geographic and climatic gradients than the SES FD metric, the general pattern was the same.

Species packing (as measured by SES NN) tended to show opposing results to that found using the other metrics. In particular four of the six traits had lower than expected nearest trait

neighbour distances in tropical assemblages with wood density and SLA being the two exceptions. Thus for the majority of the traits species were more tightly packed into trait space than expected given the species richness and global pool of trait values.

In addition to the general latitudinal trends, there was considerable longitudinal variation in the traits. For example, wood density and SLA varied more among species in tropical dry forests (Pacific Coast of Central America and north-east Brazil) than among species in wet tropical forests (Atlantic Coast of Central America and north-west Brazil) reinforcing the notions that the trait dispersion results are not simply explained by latitude and species richness. Other climatic factors, such as soil nutrient levels, disturbance and the number of days below freezing, may also be strong correlates, but they were not analysed in this work. In general, correlative analyses with climatic variables showed that, after controlling for species richness, the regions with the largest annual temperature ranges and the lowest variance in monthly precipitation totals generally exhibited lower trait dispersion in wood density, SLA, seed mass and maximum height than regions with lower temperature ranges and high variation in monthly precipitation, while leaf %N and leaf %P displayed the opposite pattern (Table 2).

Sensitivity analyses

We performed a series of sensitivity analyses to determine whether sampling heterogeneity may have biased our statistical inferences. Bias due to spatial heterogeneity in sampling was

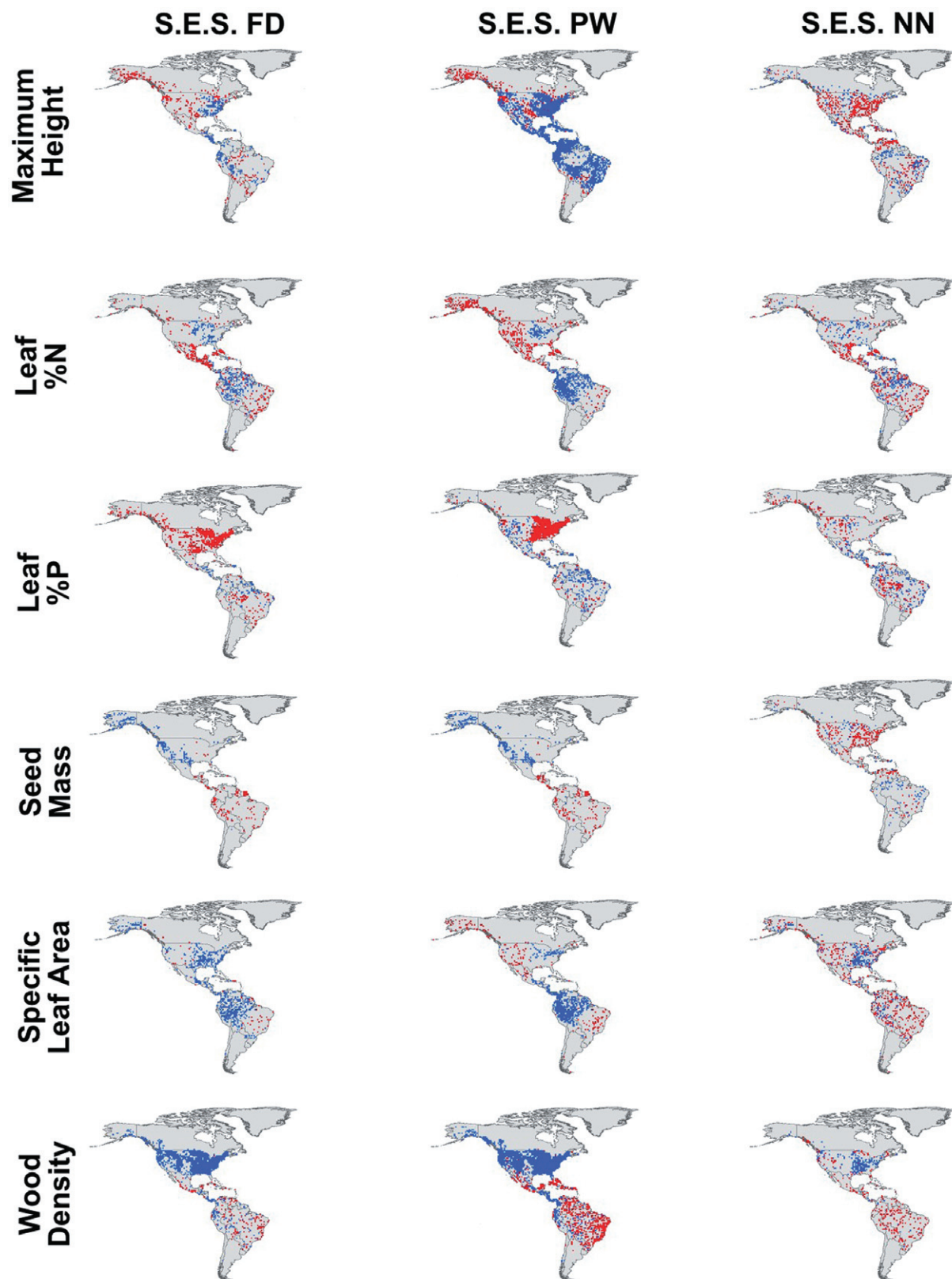


Figure 2 Maps depicting the results from the null model. Grid cells where there is greater functional trait diversity than expected given the species richness are coloured red. Grid cells where there is lower functional trait diversity than expected given the species richness are coloured blue. The first column is the standardized effect size of the functional trait diversity (SES FD), the second column is the standardized effect size of the mean pairwise trait distance (SES PW) and the third column is the standardized effect size of the mean nearest trait neighbour distance (SES NN).

estimated by re-doing all analyses at the resolution of 5° map grid cells in order to minimize artefacts due to small-scale spatial heterogeneity. It was also estimated by rarefying the sampling to include only 25 randomly selected species. In both analyses, the results from the sensitivity analyses were consistent with the results and inferences reported in the main analyses (Appendix S1–S4, Figs S1–S8, Tables S2–S4). This suggests that while spatial sampling heterogeneity does exist, it probably generated little statistical bias.

Biases due to sampling only common species in the occurrence or trait databases were estimated using tropical forest inventory plots. The results of this sensitivity analysis (Appendix S1–S4, Figs S1–S8, Tables S2–S4) show that the results generated using only the most common species in these forests are largely consistent with the results generated using the entire species lists. This result suggests that while in many cases only common species may have been sampled spatially and/or in the trait database, this sampling heterogeneity probably introduced little bias due to the lack of a correlation between species abundance and trait values.

DISCUSSION

During the past decade plant ecologists have increasingly analysed the filtering of functional traits into local-scale species assemblages in order to identify the ecological mechanisms governing community assembly (Weiher & Keddy, 1995). This research has typically focused on the general importance of abiotic filtering along local-scale environmental gradients such that in abiotically harsh environments the assemblage should contain a non-random subset of species that are more functionally similar than that expected. This has resulted in a great deal of evidence supporting the general importance of abiotic filtering driving the structure of local-scale assemblages (e.g. Weiher *et al.*, 1998; Stubbs & Wilson, 2004; Cornwell *et al.*, 2006; Kraft *et al.*, 2008; Swenson & Enquist, 2009).

Much less is known about how global pools of functional diversity are filtered into regional-scale assemblages that are ultimately then filtered into the local-scale assemblages (Algar *et al.*, 2011). It is reasonable to predict that the same mechanisms of abiotic filtering that are often uncovered in local-scale studies may also operate at much larger spatial scales. Indeed the favourability hypothesis in biogeography (Fischer, 1960) could be considered a large-scale version of the abiotic filtering hypothesis that is the focus of local-scale plant community assembly studies (Weiher & Keddy, 1995). That is, the relatively harsher temperate zone climate is expected to limit or filter the diversity or varieties or functions possible. Conversely, more climatically benign tropical regions may permit a higher diversity or variety of functions. This should generate a lower than expected functional trait diversity at one end of a continental-scale climatic gradient and a higher than expected functional trait diversity at the other end.

To our knowledge, whether global pools of functional trait diversity are non-randomly filtered into regional-scale assemblages has not been comprehensively addressed in the botanical

literature across substantial species diversity or climatic gradients and using appropriate null models. The present analyses provided this test.

Specifically, here we have combined georeferenced plant occurrence data with extensive plant functional trait databases to provide a detailed view into the distribution, diversity and filtering of woody plant functional traits in North and South America.

We find evidence for four of the six traits studied that tropical latitudes harbour levels of functional trait diversity that are higher than expected given their species richness, and that temperate latitudes tend to have even less functional trait diversity than expected when using the SES FD and SES PW metrics (Table 2). The two exceptions to this pattern were leaf %N and leaf %P. This result is also generally consistent across altitude. These results therefore generally support the prediction of the favourability hypothesis where temperate zone assemblages should be a non-randomly constrained subset of the global trait pool and tropical assemblages should be more functionally diverse than expected given the species richness.

The results from the nearest neighbour (SES NN) metric were not consistent with those from the SES FD and SES PW metrics. In particular for all traits except seed mass and wood density the nearest trait neighbour was closer than expected in the tropics and low altitudes, suggesting that species are non-randomly packed into 'trait space' in the tropics (Table 2). Thus while the overall diversity of traits is higher than expected in the tropics, species are also more tightly packed into trait space than expected.

In addition to analysing the filtering of traits along latitudinal and altitudinal gradients, we quantified trait filtering along several climatic axes as a more direct test of the favourability hypothesis. As would be expected, the filtering of traits along a gradient of mean annual temperature and temperature seasonality largely mirrors that found along the latitudinal and altitudinal gradients (Fig. 2, Table 2). Interestingly, the results show that precipitation seasonality was often positively correlated with a higher than expected level of trait diversity. This can be seen in Figure 2 where seasonal tropical forests of Brazil and Central America have a higher than expected trait diversity compared with less seasonal forests in the upper Amazon. Thus the filtering of functional trait diversity is not simply a latitudinal issue and is best considered along climatic gradients. It is important to note that this does not mean that the raw levels of functional trait diversity are lower in aseasonal tropical rain forests and higher in seasonal tropical rain forests. Rather this indicates that the trait diversity in seasonal forests is simply higher than that expected given their species richness. It seems likely that the strong precipitation seasonality in these forests permits a great variety of functional strategies to regionally co-occur.

Ultimately the results presented support the prediction of the favourability hypothesis that temperate zone assemblages should be a highly constrained functional subset of the global pool (Fischer, 1960). Under the favourability hypothesis, temperate regions are envisioned as climatically harsh not simply

because of their low temperatures but also because of their seasonality, and our results regarding temperature seasonality support this view. Interestingly, precipitation seasonality had the opposite influence on functional trait diversity suggesting that seasonality in general does not necessarily limit functional diversity. Further, leaf %P diversity consistently showed the opposite patterns across the geographic and climatic gradients studied. The contrasting nature of these patterns may be taken as evidence against the favourability hypothesis. We consider this not to be the case and that, in fact, it might well be the exception that proves the rule. In particular highly weathered tropical soils are generally depleted in phosphorus (Walker & Syers, 1976; Crews *et al.*, 1995; Vitousek & Farrington, 1997), and thus are not as favourable to plant growth as other environmental factors in the tropics. Therefore a favourability hypothesis would predict a lower than expected diversity of leaf %P values in tropical assemblages found on nutrient-poor soils.

In sum, the results show that in general the overall functional trait diversity in regional-scale tropical species assemblages in seasonal forests tends to be higher than that expected given the global pool of traits and the observed species richness. To our knowledge this is the first evidence from functional trait data and null modelling analyses that conclusively provides support for the favourability hypothesis. Further, this is evidence that gradients in abiotic filtering that are so often the focus of local-scale community assembly studies are also very important in determining the functional composition of regional-scale assemblages. Thus it would appear that similar trait filtering mechanisms are operating from global to regional to local scales. Future work that explicitly links global plant functional trait pools to regional trait pools to very localized trait pools (Algar *et al.*, 2011) will be needed to fully explore this possibility.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

- Figure S1** The geographic distribution and diversity of plant function in North and South America based upon the rarefaction analyses. The first, second, and third columns represent the functional trait diversity (FD), the mean pairwise trait distance (PW), and the mean nearest trait neighbor distance (NN) values respectively with warm colors indicating high functional trait diversity and cool colors indicating low functional trait diversity.
- Figure S2** The change in the standardized effect size results when using only the most common 5% of tree species in the 50-ha Barro Colorado Island forest dynamics plot in Panamanian lowland moist forest (far left side of x-axis) to 100% of the tree species in the forest plot (far right side of x-axis).
- Figure S3** The change in the standardized effect size results when using only the most common 5% of tree species in the 16-ha Luquillo forest dynamics plot in Puerto Rican pre-

montane rain forest (far left side of *x*-axis) to 100% of the tree species in the forest plot (far right side of *x*-axis).

Figure S4 The change in the standardized effect size results when using only the most common 5% of tree species in the 15-ha San Emilio forest dynamics plot in Costa Rican dry forest (far left side of *x*-axis) to 100% of the tree species in the forest plot (far right side of *x*-axis).

Figure S5 The change in the standardized effect size results when using only the most common 5% of tree species in the 25-ha Yasuni forest dynamics plot in Ecuadorian lowland rain forest (far left side of *x*-axis) to 100% of the tree species in the forest plot (far right side of *x*-axis).

Figure S6 The number of species in a grid cell that have trait values.

Figure S7 The proportion of the woody plant species richness in a grid cell that has a trait value attached to it.

Figure S8 WorldClim maps of altitude and climatic variables used for the correlative analyses. Temperature seasonality is the product of 100 and the standard deviation of monthly values. Annual temperature range is the annual maximum and minimum values. Precipitation seasonality is the coefficient of variation in the monthly precipitation totals.

Table S1 The size of the global functional trait databases compiled and utilized for analyses and the number of geo-referenced specimens and species in the plant occurrence database that could be assigned a trait value.

Table S2 Spearman rank correlations between the mean trait value in five degree map grid cells and physiographic and climatic variables.

Table S3 Spearman rank correlations between the dispersion of trait values in five degree map grid cells and physiographic and climatic variables.

Table S4 Spearman rank correlations between the mean dispersion of trait values from the rarefaction analyses in one degree map grid cells and physiographic and climatic variables.

Appendix S1 Additional details on methodologies and data used in this study.

Appendix S2 Sampling heterogeneity and testing for potential biases in the trait dispersion results: sensitivity to only sampling common species.

Appendix S3 Distribution of sampling intensity.

Appendix S4 Distribution of climatic variables.

Appendix S5 Additional literature used to compile the functional trait databases.

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BIOSKETCH

Nathan Swenson is an assistant professor of plant biology at Michigan State University. He is interested in the evolution of functional diversity and how it is distributed in plant assemblages through space and time. N.G.S. and J.P. designed and implemented the analyses. N.G.S., B.J.E., J.P. and A.J.K. conceived of the project. All authors assisted in the formulation of the project and the writing of the manuscript and all authors provided data.

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