	<p>filtering may only affect trait means, and thus species composition, but not species richness. We assessed geographic patterns in plant traits filtering, potential environmental drivers, and their relationships to species richness patterns using a comprehensive set of tree range maps. We focused on four key plant functional traits that reflect major life history axes (maximum height, specific leaf area, seed mass, and wood density) and four climatic variables (annual mean and seasonality of temperature and precipitation), to test for trait-based community assembly using a null model approach. We tested for significant spatial shifts in trait means and variances. While we found significant shifts in mean species' trait values at most grid cells, trait variances at most individual grid cells did not deviate from the null expectation. Measures of environmental harshness (cold, dry, seasonal climates) and lower species richness were associated with a reduction in variance of seed mass and specific leaf area. The pattern in variance of height and wood density was, however, opposite. These findings do not support the hypothesis that more stressful conditions universally limit species and trait diversity in North America. Environmental trait filtering does, however, structure assemblage composition, by selecting for certain optimum trait values under a given set of conditions.</p>

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Shifts in trait means and variances in North American tree assemblages: species richness patterns are loosely related to the functional space

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Abstract

30 One of the key hypothesized drivers of gradients in species richness is environmental
31 filtering, where environmental stress limits which species from a larger species pool gain
32 membership in a local community owing to their traits. We assessed the role of environmental
33 filtering in shaping tree assemblages across North America north of Mexico by testing the
34 hypothesis that colder and drier environments with high seasonality (stressful conditions for
35 most plant species) constrain tree trait diversity (variance) and thereby limit species richness.
36 Alternatively, environmental filtering may only affect trait means, and thus species
37 composition, but not species richness. We assessed geographic patterns in plant traits filtering,
38 potential environmental drivers, and their relationships to species richness patterns using a
39 comprehensive set of tree range maps. We focused on four key plant functional traits that
40 reflect major life history axes (maximum height, specific leaf area, seed mass, and wood
41 density) and four climatic variables (annual mean and seasonality of temperature and
42 precipitation), to test for trait-based community assembly using a null model approach. We
43 tested for significant spatial shifts in trait means and variances. While we found significant
44 shifts in mean species' trait values at most grid cells, trait variances at most individual grid
45 cells did not deviate from the null expectation. Measures of environmental harshness (cold,
46 dry, seasonal climates) and lower species richness were associated with a reduction in
47 variance of seed mass and specific leaf area. The pattern in variance of height and wood
48 density was, however, opposite. These findings do not support the hypothesis that more
49 stressful conditions universally limit species and trait diversity in North America.
50 Environmental trait filtering does, however, structure assemblage composition, by selecting
51 for certain optimum trait values under a given set of conditions.

52

53 **Key words:** environmental filtering, functional biogeography, macroecology

54 Introduction

55 A central goal of biodiversity science is to understand the ecological and evolutionary forces
56 generating and maintaining biodiversity patterns. One of the key factors hypothesized to
57 shape changes in diversity across broad environmental gradients is environmental filtering.
58 Filtering occurs when species that lack the ability to tolerate local environmental conditions
59 are precluded from gaining entrance into a given location (Diamond 1975, Weiher and Keddy
60 2001). Specifically, environmental filtering is hypothesized to act on more extreme
61 phenotypes so as to promote local convergence in plant strategies (Keddy 1992) and is,
62 therefore, expected to promote the co-occurrence of species that are more ecologically similar
63 than expected from a random sample of the species that could potentially colonize the study
64 site. Filtering is thought to regulate species richness both locally and regionally, with some
65 filters operating at specific scales and others operating across scales (Algar et al. 2011,
66 Freschet et al. 2011, Lessard et al. 2012, de Bello et al. 2013; see also Terborgh 1973).
67 Although there are numerous studies that have focused on environmental filtering at the
68 community scale along relatively small environmental gradients (e.g. Weiher and Keddy
69 1995, Kraft et al. 2008, Cornwell and Ackerly 2009, Kraft and Ackerly 2010), the effect of
70 large-scale environmental filters on diversity in plant strategies is less well understood
71 (Freschet et al. 2011, Swenson et al. 2012).

72 Studies invoking environmental filtering for explaining biodiversity patterns generally
73 make three assumptions. First, physiological tolerances of individuals are often invoked as the
74 key reason for filtering. Second, such tolerances and the resultant performances of individuals
75 are thought to be reflected in species' functional traits (McGill et al. 2006, Violle et al. 2007).
76 Consequently, more stressful environments, characterized by extreme temperatures or drought
77 conditions, are thus predicted to result in a reduction in the range or variance of species' trait
78 values from those of the larger regional species pool (Díaz et al. 1998, Weiher et al. 1998,

Cornwell and Ackerly 2009, de Bello et al. 2009, Kraft and Ackerly 2010). Third, the strength of environmental filtering will increase with increasing environmental stress associated with seasonality, extremes in temperature and precipitation, and low resource availability (Weiher et al. 1998, Stubbs and Wilson 2004, Valladares et al. 2008, Kluge and Kessler 2011). Aside from the role of environment, assemblages may be shaped by biotic interactions such as competition leading to either reduction in trait variance (convergence) or divergence in traits (Mayfield and Levine 2010; see also MacArthur and Levins 1967, Ågren and Fagerström 1984).

Despite some evidence for environmental filtering in harsh environments (assuming that cold, dry and seasonal environments are stressful for most plants; Weiher et al. 1998, Stubbs and Wilson 2004, Kluge and Kessler 2011, Swenson et al. 2012), it is unclear whether observed differences in diversity across broad-scale gradients are due to filtering rather than other processes (see Currie et al. 2004 for review). It has been suggested that the latitudinal gradient in species richness can be explained by the difference between the intensity of environmental filtering and biotic interactions (Dobzhansky 1950, Terborgh 1973, Schemske 2002). Specifically, greater species diversity under warm, humid and climatically more stable environments may result from more rapid evolution caused by more intense biotic interactions, whereas more stressful environments can reduce the number of possible ecological strategies, thus reducing species richness (Dobzhansky 1950, Schemske 2002, see also Swenson et al. 2012). Together, environmental filters and the relative intensity of biotic interactions are hypothesized to determine the total niche space available to species within a local community (Díaz and Cabido 2001, Schemske 2002). This volume of niche space available consequently limits the total number of species that are able to coexist (Chase and Leibold 2003). Assuming that functional traits can be used as proxies for niche axes (Westoby et al. 2002, Violle and Jiang 2009), measures of trait variation can provide a measure of the

volume of niche space. Indeed, at the scale of local communities variation in functional traits often increases with species richness, although the reported correlations are often weak and vary from trait to trait (Shepherd 1998, Stevens et al. 2006, Ricklefs 2009, Ricklefs and Marquis 2012), and the causality can also be also reversed (Ricklefs and Miles 1994). The extent to which the positive correlation between species richness and variation in functional traits seen at small spatial scales appears at larger scales is largely unknown (but see Roy et al. 2001).

Here, we explore the geographic variation in functional traits of trees across North America. We tested for the strength of environmental filters, the environmental factors behind them, and associations of these filters with species richness patterns. While geographic patterns in mean values reflect changes in species composition, spatial variation in the variance of trait values reflects the size of the occupied niche space. Specifically, we test the following predictions.

1. Under more harsh (cold, dry, and/or seasonal) climatic conditions, trait variance within an assemblage (grid cell) should be lower, reflecting a decrease in the available niche space. This is expected because marked climatic gradients across North America should cause strong differential environmental filtering with shifts in both trait means and variances along geographic stress gradients.
2. Stress-driven gradients in niche space determine richness of woody species, so that grid cell trait variance should positively correlate with assemblage species richness.

Methods

Species data

We used the USGS tree range maps dataset (<http://esp.cr.usgs.gov/data/atlas/little/>) for the USA and Canada initially compiled by Little (Little 1971, 1976, 1977, 1978). We overlaid each range with an equal-area spatial grid corresponding to 1° of latitude and longitude at the

equator (app. $111 \times 111 \text{ km}^2$). For our analyses we only included cells with centroids inside the continent (2206 cells). We updated old taxonomic names and merged distributional ranges of those species that are currently considered as subspecies or synonyms according to The Plant List (Release 1.0; <http://www.theplantlist.org/>). The total number of species with accepted names and having their range within the grid was thus 604 (out of the 679 from the original dataset).

Traits

Expanding on the three-dimensional Westoby's LHS schema (leaf-height-seed; Westoby 1998, Westoby et al. 2002), we focused on four traits that together describe the major life history and ecological strategies of trees: specific leaf area, maximum plant height, seed mass, and wood density. Values of specific leaf area result from a trade-off between long leaf lifespan, structural strength and reduction of nutrient leaching vs. high net photosynthetic capacity, fast growth and better competitive ability (Chabot and Hicks 1982, Reich et al. 1997, 1998, Wright et al. 2004). Maximum height represents the potential shading capacity of crown and it is related to competition (Falster and Westoby 2003). Values of seed mass result from the trade-off between production of few large seeds (each containing more resources) versus many small seeds (each containing small resources), which influences dispersal ability, shade tolerance, and seedling survival (Westoby et al. 1992, Moles and Westoby 2006). Wood density is a key functional trait for trees representing the trade-off between the short-term gain versus mechanical strength, chemical defense, efficiency of water transport, and low mortality rate (Enquist et al. 1999, Hacke et al. 2001, Baas et al. 2004, Swenson and Enquist 2007, Chave et al. 2009). We used a compilation of data for these traits assembled from the literature and published datasets included in the BIEN database (Botanical Information and Ecology Network; Enquist et al. 2009; <http://bien.nceas.ucsb.edu/bien/>) which integrates

georeferenced plant observations from herbarium specimens, vegetation plot inventories, species distributions maps, and plant traits for plants of the New World. For a given trait, we then calculated the mean and variance across all species in each grid cell. This calculation was based only on species with known trait values (see Supplementary material Appendix 1 for statistical details and maps of the distribution of missing trait data proportional to the number of species).

Climate

We used mean annual temperature, annual precipitation, temperature seasonality, and precipitation seasonality from the Worldclim database (www.worldclim.org; resolution 30"; Hijmans et al. 2005) as the basic descriptors of the environmental conditions. We defined environmental harshness as low temperature and/or precipitation and high seasonality, as these conditions are stressful for most plant species. We calculated mean values of these variables for each grid cell.

Null models

In order to test whether the variance and mean in trait values per sample is significantly higher or lower than expected, given the species richness, we standardized these values by performing a series of randomizations. Specifically, we used the standardized effect size measure (SES; Gotelli and McCabe 2002, see also Swenson and Enquist 2009, Jung et al. 2010, Kraft and Ackerly 2010) defined as

$$SES = (I_{obs} - I_{exp}) / SD_{exp} \quad [1]$$

where I_{obs} is the observed mean or variance of the trait values, I_{exp} is the simulated mean or

variance of the trait values calculated from the random selection of species from the species pool, and SD_{exp} is the standard deviation of the simulated values. Thus, high SES values indicate greater variance (or mean) than expected from the observed number of species and low SES values indicate lower variance (or mean) than expected. The probability that I_{obs} does not differ from the value expected by chance can be tested by comparing I_{obs} with the distribution of simulated values.

In order to quantify this probability and test for the significance in environmental filtering, we estimated means and variances in the trait values using SES models with 999 permutations. Given that the null distributions of trait means and variances follow a normal distribution, we considered as significant those samples that had their SES trait values higher or lower than 1.96, which corresponds to the 95 percent confidence interval of the two-tailed distribution. We tested for the normality in the null distributions using the Shapiro-Wilk test (Royston 1982), and in order to approach the normal distribution, we log-transformed values of height, wood density and seed mass using the natural logarithm. We defined the species pool as the set of all North American tree species present in our dataset.

Given the evolutionary difference between angiosperms and gymnosperms (Graham 1999), we repeated all analyses for only angiosperm data. All analyses were scripted in R (version 2.15; R Development Core Team 2012).

Statistical analyses

We tested for correlations between mean and variance in trait values and both the climatic variables and the log_e-transformed number of species using Pearson's correlation coefficients. We calculated the significance of these relationships using Dutilleul's method in SAM (Spatial Analysis in Macroecology; Rangel et al. 2006). This method estimates p-values based on the degrees of freedom corrected for the spatial autocorrelation (Dutilleul 1993). We calculated

these correlations using both standardized (SES) trait values and non-standardized (raw) traits.

Results

Assemblage trait mean values

Mean trait deviated strongly from those expected from random sampling of the species pools, indicating filtering effects on functional composition (Table 1, Fig 1A). Means of seed mass and wood density followed a latitudinal gradient with significantly lower values than expected at high latitudes. Mean specific leaf area followed a longitudinal gradient with values higher than expected in eastern deciduous forests, and with lowest values in southwestern deserts. Mean height was higher than expected on the Pacific coast and in southeastern deciduous forests, and lowest in woody species assemblages of south-western deserts and in the northern most boreal forests of Canada, Alaska and Newfoundland. These results were qualitatively the same when conifers were excluded from the analysis (Supplementary material Appendix 2).

Assemblage trait variance values

In contrast to the strong evidence for filtering-driven shifts in trait means, non-random spatial shifts in trait variances were consistently rarer. We found some evidence of trait divergence (higher variance than expected) only for height and seed mass (Table 1, Fig. 1B, 2A,C). There was strong trait convergence (i.e., lower variance than expected) for wood density, and no significant convergence for specific leaf area, seed mass, and height (Table 1, Fig. 1B, 2B,C,D). Nevertheless, the significance of convergence in wood density was partly affected by variation in SD_{exp} as the non-standardized variance in wood density (I_{obs}) did not vary strongly with the number of species in a sample (Fig. 2D). These results were qualitatively the same when conifers were excluded from the analysis (Supplementary material Appendix 2).

230

231 *The relationship between assemblage trait variation and climate*

232 To be consistent with the analyses concerning trait variance, we present here only the results
233 based on the SES trait means, though the results based on non-standardized trait means, were
234 qualitatively the same (Supplementary material Appendix 3). Standardized effect size of mean
235 height and specific leaf area strongly increased with precipitation and weakly decreased with
236 precipitation seasonality (Table 2). Standardized effect size of both mean wood density and
237 mean seed mass increased with temperature, although this relationship was not significant for
238 wood density. In agreement with the stronger geographic pattern of non-random convergence
239 in values of wood density (Fig. 1B), we found strong correlation between the SES variance in
240 wood density and climatic variables. Nevertheless, in contrast to our prediction, this variance
241 increased with increasing environmental harshness (defined as cold or dry climate with high
242 seasonality). On the other hand, SES variance in specific leaf area and seed mass decreased
243 towards increasing environmental harshness, despite the non-significant spatial pattern of
244 convergence in these traits (Table 1, Fig. 1B, 2B,C). SES variance in specific leaf area
245 increased significantly with increasing precipitation whereas SES variance in seed mass
246 strongly increased with increasing temperature. We obtained similar results when using only
247 angiosperm data (Supplementary material Appendix 2) and non-standardized variances
248 (Supplementary material Appendix 3).

249

250 *The relationship between assemblage trait composition and species richness*

251 SES variance in height and wood density decreased with the increasing number of species
252 whereas SES variance in seed mass and specific leaf area increased with species richness
253 (Table 2, Fig. 2). Most of these relationships were consistent with those obtained using non-
254 standardized variances in trait values (Fig. 2, Supplementary material Appendix 3). All trait

mean values except of wood density correlated positively with the number of species. It thus seems that environmental filters responsible for variation in trait means are also important for species richness.

Discussion

Shifts in mean trait values were strongly correlated with climate, in accord with our prediction. Geographical patterns in mean assemblage trait values varied independently among traits. Mean height and specific leaf area followed the longitudinal precipitation gradient, whereas mean wood density and seed mass varied with the latitudinal temperature gradient. The patterns are in accord with previous large-scale studies (Swenson and Enquist 2007, Chave et al. 2009, Moles et al. 2009, Swenson and Weiser 2010, Swenson et al. 2012). Tall trees were present only in sites with sufficient water availability, corresponding to the trade-off between plant height and drought tolerance (Ryan et al. 2006, Moles et al. 2009). Woody species growing in dry conditions had a low specific leaf area, since small and thick cells, that are more tightly packed and can thereby reduce water loss (Poorter et al. 2009). The increase in seed mass with temperature may correspond to the increase in competition intensity leading to a higher investment in initial growth of individual seedlings (Moles and Westoby 2006). The decrease in mean wood density with decreasing temperature could be due to the decrease in flow rate of water through stems (Roderick and Berry 2001).

The observed significant shifts in mean trait values imply that climate may indeed be a key factor for trait filtering at the continental scale. Nevertheless, we found only limited support for the decrease in trait variance with increasing environmental harshness (the case of the seed mass and specific leaf area). Moreover, this reduction in trait variance was not significant when comparing trait variance within individual grid cells to the null variance based on the random selection of species from the species pool. Our results appear to

contradict recent work by Swenson et al. (2012) who found strong significant evidence for both convergence and divergence in most traits of tree communities across the New World. However, differences between our study and their's are likely due to differences in the size of the species pool used in the null models (Lessard et al. 2012). The contrast between the temperate and tropical zone is obviously greater relative to the variation in traits within temperate North America. Our results suggest that the filtering pattern observed in Swenson et al. (2012) occurs only at very large spatial scales - between tropical and temperate taxa, but not within the species pool of North America.

The means of most trait values of co-occurring species decreased towards harsh environments, defined here as cold or dry climates with high seasonality, and this decrease was associated with a decrease in species richness. Increasingly more seasonal and extreme environments thus select for different phenotypes. In contrast with our prediction, variance in height and wood density decreased neither with increasing environmental harshness, nor with decreasing species richness. This could be due to the fact that trees in warm and wet environmental conditions have higher mean biomass and appears to be more influenced by competition for light. Small woody plants and trees with higher mortality rates are more disadvantaged, leading to constrained variation in maximum height and wood density. The fact that we did not find strong evidence for an increase in the number of species with the increase in total niche space (represented by the variance in trait values) can again be a consequence of tree species richness peaking at conditions suitable for dense forests. Competitive hierarchies can thus be an important factor shaping trait distributions in large-scale species assemblages (Mayfield and Levine 2010, Araújo and Rozenfeld 2014). Unlike variance in height and wood density, variance in specific leaf area and seed mass increased with species richness. This indicates that specific leaf area and seed mass may be important traits for niche differentiation allowing coexistence of more species.

The fact that we did not find evidence for significant convergence and divergence in traits at individual grid cells (assemblages) could be caused by our selection of traits. Species may differ in other aspects than those represented by the few selected essential traits (e.g. frost or drought tolerance, see Stahl et al. 2013, Hawkins et al. 2014). Nevertheless, given that the traits we used are supposed to represent the main plant strategy axes (Westoby 1998, Westoby et al. 2002), species' abilities to tolerate frost and drought should be reflected in these traits (e.g. Reich et al. 1997, Roderick and Berry 2001, Koch et al. 2004, Wright et al. 2004, Chave et al. 2009). It is also possible that traits measured directly at a site may be more suitable for estimating actual trait convergence or divergence than using taxon averages from database (Albert et al. 2011, Violle et al. 2012). Similarly, including intraspecific trait variation could potentially increase the evidence for significant filtering at the plot scale (Albert et al. 2011, Violle et al. 2012). Such data are, however, not available for large scales. Another possibility is that certain environments select for phenotypes with specific combinations of trait values rather than single traits. Filtering can thus operate on multiple traits simultaneously. Nevertheless, it seems that functional volume computed using multiple traits thought to represent the main plant strategy axes does not decrease with increasing environmental stress, nor does it increase with species diversity (Ricklefs 2012).

In conclusion, we did not find strong evidence that increasingly harsh or more stressful environments considerably reduce the variance in trait values of co-occurring trees in North America. Convergence in trait values was associated with an increase in environmental harshness and decrease in species richness only for some traits and individual grid cells did not show strong pattern of non-random convergence or divergence when comparing to the species pool. Instead, we found strong evidence for significant spatial shifts in the means of trait values, and these trends were driven by climate. This indicates that environmental trait filtering does affect assemblage composition by selecting for certain optimum trait values

under a given set of conditions.

Acknowledgements

This work was conducted as a part of the Botanical Information and Ecology Network (BIEN) Working Group (PIs BJE, Richard Condit, BB, SD, RKP) supported by the National Center for Ecological Analysis and Synthesis, a center funded by NSF (Grant #EF-0553768), the University of California, Santa Barbara, and the State of California. The BIEN Working Group was also supported by iPlant (National Science Foundation #DBI-0735191; URL: www.iplantcollaborative.org). IS was funded by grant No. P505/11/2387 from the Grant Agency of The Czech Republic and by a Fulbright fellowship. CV was supported by a Marie Curie International Outgoing Fellowship within the 7th European Community Framework Program (DiversiTraits project, no. 221060). JCS was also supported by the European Research Council (ERC-2012-StG-310886-HISTFUNC). NM-H acknowledges supported by an EliteForsk Award and the Aarhus University Research Foundation. JCD and BB were supported by the NSF-funded iPlant Collaborative. We thank Yue Max Li for creating the grid we used for overlaying tree ranges.

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For Review Only

Biosketch. IS is a postdoctoral researcher interested in macroecology, biodiversity and mechanisms generating species richness patterns in plants at various spatial scales. Author contributions: IS, CV, BJE and NJBK designed the study; IS analysed the data, IS led the writing with major contributions from CV, NJBK, BJE, DS, and JC-S; BJE, RKP, BB, BT, J-CS, PMJ, MS, SKW, JR, JCD, NM-H, NJBK, BJM, WP, and NS developed the BIEN database (<http://bien.nceas.ucsb.edu/bien/>). All authors discussed and commented on the manuscript.

517 **Tables**

518 Table 1: Proportion of grid cells having mean or variance of trait values significantly higher or
519 lower than expected by chance. See Fig. 1 for spatial patterns.

Proportion of significance				
	Lower than random		Higher than random	
	Mean	Variance	Mean	Variance
Height	0.061	<0.001	0.103	0.109
Specific leaf area	0.009	0	0.204	0
Seed mass	0.679	0	0.055	0.035
Wood density	0.437	0.219	0.007	<0.01

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Table 2: Pearson's correlation coefficients between environmental variables, number of species, and standardized effect size (SES) of means and variances in trait values at different spatial scales. Significance ($p < 0.05$) is highlighted in bold.

	Temperature	Precipitation	Temperature seasonality	Precipitation seasonality	Ln(no of species)
MEAN					
Height	0.552	0.669	-0.478	-0.418	0.723
Specific leaf area	0.140	0.477	-0.022	-0.313	0.543
Seed mass	0.722	0.511	-0.485	-0.249	0.504
Wood density	0.459	0.087	-0.188	0.162	0.035
VARIANCE					
Height	-0.544	-0.178	0.364	0.037	-0.392
Specific leaf area	0.376	0.380	-0.241	-0.276	0.547
Seed mass	0.523	0.192	-0.324	-0.003	0.441
Wood density	-0.325	-0.621	0.258	0.578	-0.738

Figure legends

Figure 1. Geographic patterns of values of (A) trait mean and (B) trait variance in tree assemblages in North America: the first column represents patterns of raw (non-standardized) mean or variance in trait values, the second column shows standardized effect size (SES) of mean or variance of trait values, and the third column shows SES mean or variance of trait values that are significantly higher (red), lower (blue) than expected by chance or indistinguishable from random pattern (gray). See Table 1 for the proportion statistics.

Figure 2. The relationship between the non-standardized variation in trait values for particular traits and the distribution of the expected values from randomizations against the number of species in tree assemblages in North America. Solid lines represent confidence intervals and dashed line is the expected variance in trait values from the SES method. A decrease in the SES of a trait with species diversity indicates more convergence of trait values (A,D; height and wood density) with increased diversity, while a positive relationship indicates more divergence in assemblage trait value (B,C; specific leaf area and seed size) with increased diversity.

Figure 1

550

Figure 2

Continental-scale shifts in trait means and variances in North American tree assemblages: niche space is not universally narrower in harsh environment

Supplementary material

Appendix 1

Table A1: Number of species with known species-level traits.

Trait	Species-level trait values
Height	468
Specific leaf area	200
Seed mass	396
Wood density	218

Figure A1. Maps of distribution of species with missing trait values proportional to the total number of species present in each grid cell.

Appendix 2

Geographic patterns of mean and variance of trait values for angiosperms.

Figure B1: Geographic patterns of (A) mean and (B) variance of trait values for angiosperms: the first column represents patterns of raw (non-standardized) mean or variance in trait values, the second column shows standardized effect size of mean or variance of trait values, and the third column shows standardized effect size of mean or variance of trait values that are significantly higher (red) than expected by chance, lower (blue) than expected by chance or indistinguishable from random pattern (gray).

Table B1: Pearson's correlation coefficients between environmental variables and standardized effect size (SES) of means and variances in trait values of angiosperms. Significance ($p < 0.05$) is highlighted in bold.

	Temperature	Precipitation	Temperature seasonality	Precipitation seasonality	Ln(no of species)
MEAN					
Height	0.552	0.669	-0.478	-0.418	0.641
Specific leaf area	0.140	0.477	-0.022	-0.313	0.268
Seed mass	0.722	0.511	-0.485	-0.249	0.846
Wood density	0.459	0.087	-0.188	0.162	0.641
VARIANCE					
Height	-0.544	-0.178	0.364	0.037	-0.373
Specific leaf area	0.376	0.380	-0.241	-0.276	0.536
Seed mass	0.523	0.192	-0.324	-0.003	0.575
Wood density	-0.325	-0.621	0.258	0.578	0.292

Appendix 3

Pearson's correlation coefficients of the relationships between climate and the number of species, using non-standardized mean and variance of trait values.

Table C1: Pearson's correlation coefficients of the relationships between climate and the number of species, using non-standardized mean and variance of trait values.

	Trait	Temperature	Precipitation	Temperature seasonality	Precipitation seasonality	Ln(no of species)
MEAN	Height	0.553	0.511	-0.465	-0.320	0.732
	Specific leaf area	0.139	0.477	-0.021	-0.311	0.541
	Seed mass	0.880	0.596	-0.655	-0.338	0.772
	Wood density	0.770	0.370	-0.474	-0.084	0.530
VARIANCE	Height	-0.535	-0.213	0.407	0.059	-0.456
	Specific leaf area	0.336	0.358	0.297	-0.263	0.484
	Seed mass	0.670	0.201	-0.464	-0.011	0.523
	Wood density	0.456	-0.001	-0.351	0.112	0.135