Research

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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One of the key hypothesized drivers of gradients in species richness is environmental filtering, where environmental stress limits which species from a larger species pool gain membership in a local community owing to their traits. Whereas most studies focus on small-scale variation in functional traits along environmental gradient, the effect of large-scale environmental filtering is less well understood. Furthermore, it has been rarely tested whether the factors that constrain the niche space limit the total number of coexisting species. We assessed the role of environmental filtering in shaping tree assemblages across North America north of Mexico by testing the hypothesis that colder, drier, or seasonal environments (stressful conditions for most plants) constrain tree trait diversity and thereby limit species richness. We assessed geographic patterns in trait filtering and their relationships to species richness pattern using a comprehensive set of tree range maps. We focused on four key plant functional traits reflecting 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). We tested for significant spatial shifts in trait means and variances using a null model approach. While we found significant shifts in mean species' trait values at most grid cells, trait variances at most grid cells did not deviate from the null expectation. Measures of environmental harshness (cold, dry, seasonal climates) and lower species richness were weakly 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 filtering does, however, structure assemblage composition, by selecting for certain optimum trait values under a given set of conditions.

A central goal of biodiversity science is to understand the ecological and evolutionary forces generating and maintaining biodiversity patterns. One of the key factors hypothesized to shape changes in diversity across broad environmental gradients is environmental filtering. Filtering occurs when species that lack the ability to tolerate local environmental conditions are precluded from gaining entrance into a given location (Diamond 1975, Weiher and Keddy 2001). Specifically, environmental filtering is expected to promote the co-occurrence of species that are more ecologically similar than expected from a random sample of the species that could potentially colonize the study site (Keddy 1992). Filtering is thought to regulate species richness both locally and regionally, with a potentially stronger effect of climate at regional and continental scales, and topography, soil characteristics and land management at finer scales (Algar et al. 2011, Freschet et al. 2011, Lessard et al. 2012, de Bello et al. 2013; see also Terborgh 1973). Although there are numerous

studies that have focused on environmental filtering at the community scale along relatively small environmental gradients (Weiher and Keddy 1995, Kraft et al. 2008, Cornwell and Ackerly 2009, Kraft and Ackerly 2010), the effect of large-scale environmental filtering on diversity in plant strategies is less well understood (Freschet et al. 2011, Swenson et al. 2012, Coyle et al. 2014).

Studies invoking environmental filtering for explaining biodiversity patterns generally make three assumptions. First, physiological tolerances of individuals are often invoked as the key reason for filtering. Second, such tolerances and the resulting performances of individuals are thought to be reflected in species' functional traits (McGill et al. 2006, Violle et al. 2007, Violle and Jiang 2009). Consequently, more stressful environments, characterized by extreme temperatures or drought conditions, are thus predicted to result in a reduction in the range or variance of species' trait 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, local biotic interactions such as competition, herbivory or host-pathogen coevolution can modulate these patterns since they can lead to either reduction in trait variance (convergence) or divergence in traits within an assemblage (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 or 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 severe and seasonal climate result in evolution of a few generalized species adapted to wide range of environmental conditions (Dobzhansky 1950, Schemske 2002). Together, environmental filtering and the relative strength of biotic interactions are hypothesized to determine the total niche space available to species within a local community (Díaz and Cabido 2001, Schemske 2002). The total available niche space is consequently expected to limit the total number of species that are able to coexist (Chase and Leibold 2003, Ricklefs 2012). Assuming that functional traits can be used as proxies for niche axes (Westoby et al. 2002, Violle and Jiang 2009), the range or variance of uni- or multivariate trait space can provide an accurate measure of the volume of niche space. Indeed, at the scale of local communities variation in functional traits (expressed by different metrics) 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 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 filtering, its climatic drivers, and the consequences for the regulation of species richness in grid cells. While geographic patterns in mean values reflect species turnover, i.e. changes in species composition, spatial variation in the variance of trait values should reflect the size of the occupied niche space. Although some pioneering studies have found significant evidence for an increase in trait variance towards warm and wet conditions across North and South America (Swenson and Weiser 2010, Swenson et al. 2012), this increase was rather weak and potentially biased by the large size of the species pool used in the randomizing procedure while standardizing trait variances. Indeed, a recent study focusing on tree trait variation of forest plots within eastern United States did not find strong evidence for filtering of trait variances towards stressful conditions (Coyle et al. 2014). Furthermore, the link between environmental filtering, trait variance and species richness, while widely acknowledged (Swenson et al. 2012), has not been thoroughly tested yet.

Expanding on the three-dimensional Westoby's LHS schema (leaf–height–seed; Westoby 1998) based on specific leaf area, tree canopy height and seed mass, we added wood density to the list of traits of interest in our study. Although there are other potentially important functional traits, the LHS scheme represents functionally independent orthogonal trait axes (Westoby 1998, Westoby et al. 2002) with wood density as an additional but key functional trait for trees (Chave et al. 2009). Values of specific leaf area result from a trade-off between long leaf lifespan and slow growth on one side versus fast growth and better competitive ability on the other side (Chabot and Hicks 1982, Reich et al. 1997, 1998, Wright et al. 2004). Trees with high specific leaf area should be favored at sites with sufficient resource supply. Maximum height is related to competition for light (Falster and Westoby 2003) and it should be primarily constrained by water stress (Ryan and Yoder 1997). Values of seed mass result from the trade-off between production of few large seeds versus many small seeds, which influences dispersal and seedling survival (Westoby et al. 1992, Moles and Westoby 2006). Seed mass should be higher under warm conditions due to the higher metabolic costs of plant growth and maintenance at high temperatures (Murray et al. 2004) and due to the prevalence of animal dispersal (Howe and Smallwood 1982). Wood density represents the trade-off between the short-term gain versus mechanical strength (Enquist et al. 1999, Baas et al. 2004). Values of wood density should be constrained by low temperature (Roderick and Berry 2001).

We focused on single traits in response to single environmental variables and tested the following predictions. 1) Under more harsh (cold, arid, or seasonal) climatic conditions, trait variance within an assemblage (grid cell) should

be lower than expected from the regional species pool, 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 gradients of stress. 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. 3) Assemblage mean and variance of height should be primarily constrained by decreasing water availability; mean and variance of wood density should decrease with decreasing mean annual temperature whereas assemblage mean and variance of specific leaf area and seed mass should decrease with increasing stress from both drought and coldness.

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 (approx. 111×111 km). For our analyses we only included cells with centroids inside the continent (2206 cells, where 2095 cells contained more than 80% of land area inside the cell). We used this criterion in order to capture the unique habitats along the coast (tropical forest or marine west coast forest). 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; <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

We used a compilation of data for 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 distribution maps, and plant traits for plants of the New World. In case of multiple records, we calculated mean trait value for each species. For a given trait, we then calculated the mean and variance across all species in each grid cell (mean and variance of an assemblage). This calculation was based only on species with known trait values (see Supplementary material Appendix 1, Table A1, Fig. A1–2 for statistical details and maps of the distribution of missing trait data in absolute numbers and proportional to the number of species). We used raw variance, i.e. not corrected for trait means, because we expect the absolute variance to be the main driver of species richness (see Supplementary material Appendix 2, Fig. B1 for the plots of trait variances as functions of trait means).

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 calculated mean values of these variables for each grid cell. Values of the mean annual temperature per grid cell ranged from –14 to 24°C with the mean value of 3°C, annual precipitation varied from 88 to 2455 mm with the mean value of 647 mm. The range of values of temperature seasonality (standard deviation × 100) was 323–1628 with the mean value of 1052. Precipitation seasonality (coefficient of variation) ranged between 7 and 93 with the mean of 41. We defined environmental harshness as low temperature, low precipitation or high seasonality, as these conditions are stressful for most plant species.

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

$$SES = (I_{obs} - I_{exp})/SD_{exp} \qquad (1)$$

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 sampled from the species pool (the same number as was used to estimate the I_{obs}), 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 define the species pool as all tree species that could potentially colonize a given site. Therefore, we split North America into 6 main vegetation ecoregions using the classification published in Commission for Environmental Cooperation (1997). These 6 ecoregions were: Tundra, Taiga (merged with Northern forest and Hudson plain), Northwestern forested mountains (merged with the Marine west coast forest),
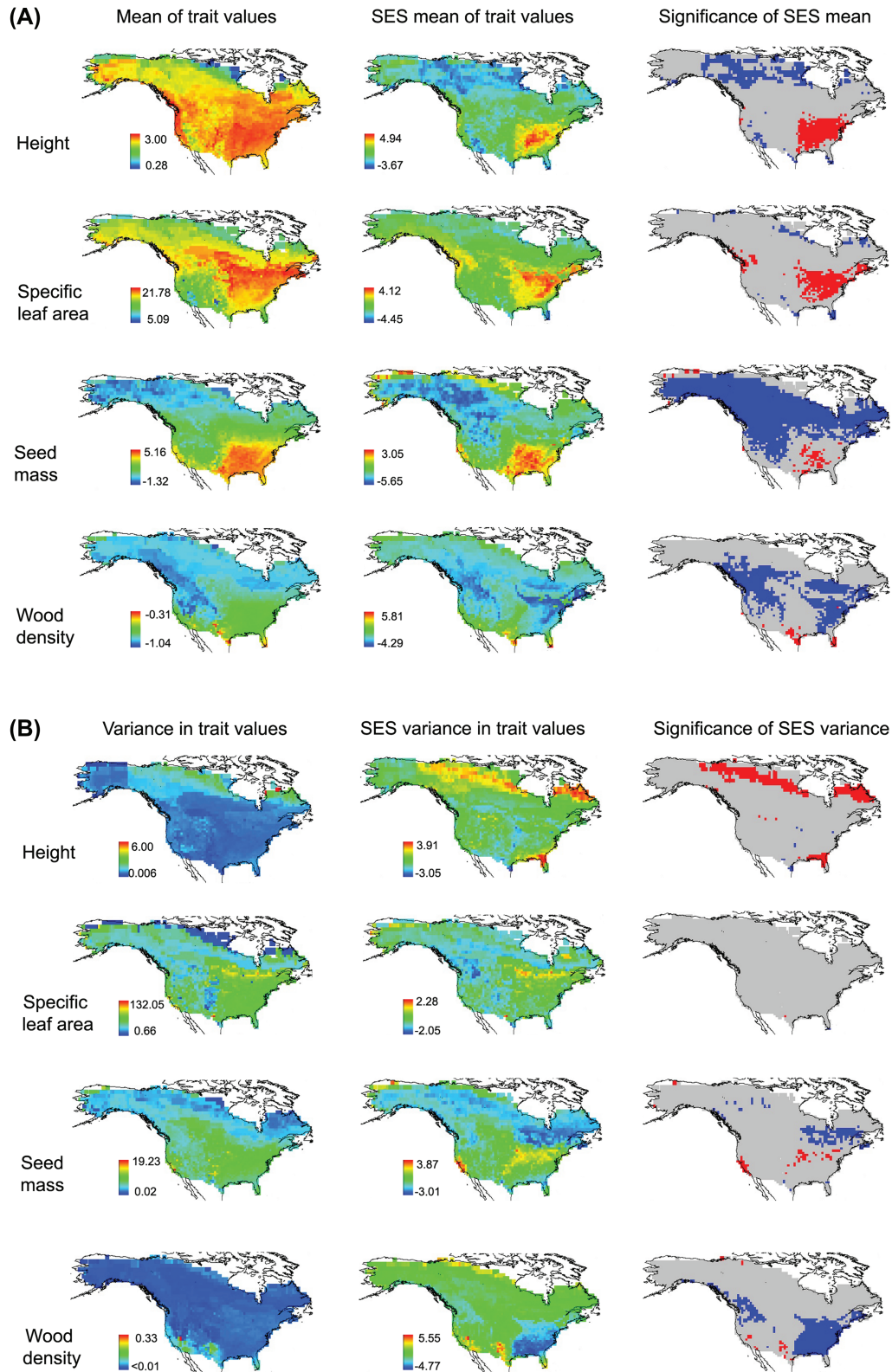
Figure 1. Geographic patterns of values of (A) trait mean and (B) trait variance in tree assemblages in North America: the first column represents patterns of raw (non-standardized) mean or variance in trait values, the second column shows standardized effect size (SES) of mean or variance of trait values, 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.

Eastern temperate forests (merged with Tropical forests), Great plains, and Desert (merged with Sierras, Semi-arid highlands and Mediterranean). We assigned each cell to the ecoregion that covered the majority of the cell area. Each of the 6 species pools was represented by the list of species occurring in the cells of a particular ecoregion. Additionally, we also performed these null model analyses using only one species pool of all North American trees.

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

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 modified t-test function in R (package SpatialPack; Cuevas et al. 2013). 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. The relationship between trait metrics (means and variances) and climate can be complex, including interactions between variables and nonlinear responses – namely higher temperature generally represents favorable conditions for plants, but not when combined with low precipitation. Therefore, we performed multiple regression with trait mean or variance as response variables against all environmental variables (linear and quadratic terms), and with an interaction term between temperature and precipitation. We chose ANOVA type III approach in order to test for the presence of a main effect after the other main effects and the interaction were accounted for (function Anova in package car; Fox and Weisberg 2011). This approach does not depend on the order of explanatory variables in the regression model.

Results

Spatial patterns of assemblage trait mean and variance values

Means of trait values deviated strongly from those expected from random sampling of the species pools, indicating a significant functional turnover, i.e. filtering effects on functional composition (Table 1, Fig. 1A). In contrast to the strong evidence for filtering-driven shifts in trait means, non-random spatial shifts in trait variances were rarely observed. The proportion of grid cells in which we detected significant shift in mean values ranged from 26 to 64%, whereas proportion of grid cells with non-random trait variances ranged from less than 1 up to 23%, There was strong trait convergence (i.e. lower variance than expected) for wood density, some trait convergence for seed mass, and almost no significant convergence for specific leaf area and height (Table 1, Fig. 1B, see Supplementary material Appendix 3, Fig. C1

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

	Lower than random		Higher than random	
	Mean	Variance	Mean	Variance
Height	0.121	0.005	0.124	0.111
Specific leaf area	0.248	< 0.001	0.137	< 0.001
Seed mass	0.603	0.071	0.038	0.029
Wood density	0.312	0.216	0.019	0.010

for relationships between non-standardized and expected trait variances against the number of species). In addition, we found some evidence of trait divergence (higher variance than expected) only for height and seed mass (Table 1, Fig. 1B, Supplementary material Appendix 3, Fig. C1). These results were qualitatively the same when conifers were excluded from the analysis (Supplementary material Appendix 4, Fig. D1) and when we used the species pool of all North American trees in the null models (Supplementary material Appendix 5, Fig. E1). In the latter case, the significant convergence in seed mass did not occur anymore.

The relationship between assemblage trait variation and climate

To be consistent with the analyses concerning trait variance, we present here only the results based on the SES trait means, though the results based on non-standardized trait means were qualitatively the same (Supplementary material Appendix 6, Table F1). Standardized effect size of mean height and specific leaf area strongly increased with increasing precipitation and temperature, and decreased with increasing seasonality of both temperature and precipitation (Table 2). Standardized effect size of mean seed mass increased with temperature, whereas increase in SES mean of wood density was best explained by the increase in precipitation seasonality. In agreement with the stronger geographic pattern of non-random convergence in values of wood density (Fig. 1B), we found strong correlation between the SES variance in wood density and climatic variables (Table 2). However, in contrast to our prediction, this variance increased with increasing environmental harshness (defined as cold, dry, or seasonal climate). On the other hand, SES variance in specific leaf area and seed mass decreased towards increasing environmental harshness. This relation was, however, rather weak for specific leaf area, in accord with the non-significant spatial pattern of convergence or divergence in this trait (Table 1, Fig. 1B, Supplementary material Appendix 3, Fig. C1). These results largely held when using only angiosperm data (Supplementary material Appendix 4, Table D1). Correlations between non-standardized variances and climate were in general stronger (Supplementary material Appendix 6, Table F1). Still, they did not qualitatively differ from those based on standardized values, except of the non-standardized variance in wood density that strongly increased with increasing temperature and decreasing temperature seasonality. The results from the multiple regression showed that the variation in means and variances in trait values was driven by multiple environmental factors, although

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	log (species richness)
Mean					
Height	**0.557**	**0.649**	−0.465	**−0.419**	**0.655**
Specific leaf area	**0.415**	**0.539**	**−0.419**	**−0.440**	**0.674**
Seed mass	**0.624**	0.475	−0.464	−0.194	0.415
Wood density	0.262	−0.159	−0.144	**0.357**	−0.189
Variance					
Height	−0.315	−0.021	0.266	−0.085	−0.202
Specific leaf area	0.132	0.229	0.010	−0.198	0.229
Seed mass	**0.494**	0.067	−0.362	0.097	0.295
Wood density	−0.272	**−0.544**	0.253	**0.537**	**−0.645**

the explanatory variables of highest importance were often the same as were the best correlates of means or variances in particular trait (compare Table 2 and Supplementary material Appendix 7, Table G1, 2). Still, there were some noteworthy differences between these results (correlations with single climatic variables vs multiple regression results). First, mean specific leaf area, seed mass and wood density, and variance in height were all best explained by the quadratic term of temperature, where the former relationship was convex and the latter three were concave (Fig. 2). Second, variance in specific leaf area was best explained by the quadratic term of temperature seasonality and variance in seed mass was best explained by the quadratic term of precipitation seasonality (Fig. 2, Supplementary material Appendix 7, Table G2). Third, the interaction between temperature and precipitation was the best explanatory variable for the mean height and variance in wood density and the second best predictor for mean specific leaf area and variance in seed mass (Supplementary material Appendix 7,

Table G1–2). Mean height increased with annual precipitation more steeply at warmer sites, whereas the increase in mean specific leaf area with precipitation was stronger at colder sites (Fig. 3, Supplementary material Appendix 7, Fig. G1). Variance in wood density steeply decreased with precipitation only at warm sites (Fig. 3).

The relationship between assemblage trait composition and species richness

SES variance in height and wood density decreased with the increasing number of species whereas SES variance in seed mass and specific leaf area increased with species richness (Table 2). Nevertheless, the correlation with species richness was strong and significant only in case of the variance in wood density. In contrast, when using non-standardized variances in trait values, there was weak and non-significant increase in variance in wood density. All other relationships
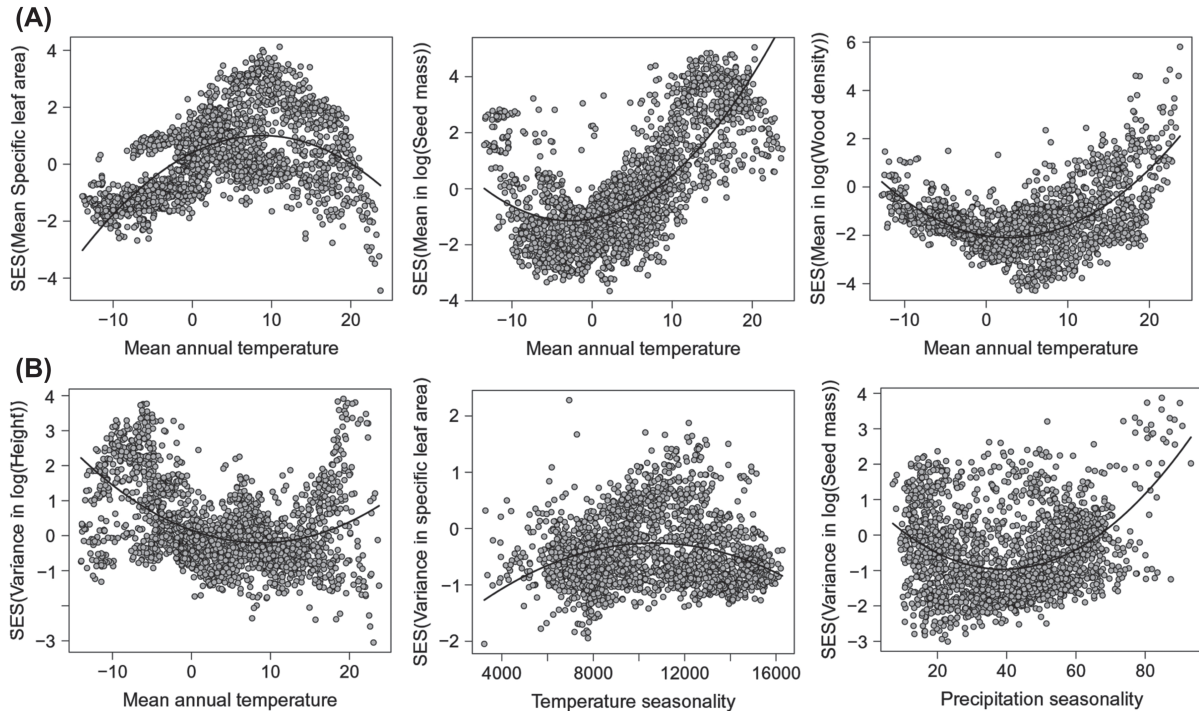

Figure 2. Relationships between trait means (A) or variances (B) and their best explanatory variable from the multiple regression (see Supplementary material Appendix 7, Table G1–2 for multiple regression results).
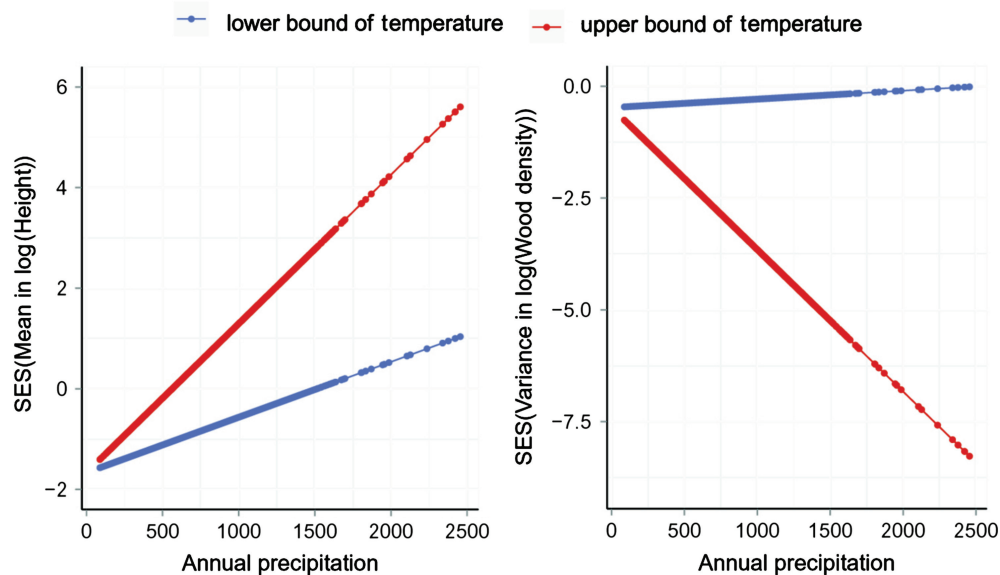
Figure 3. The effect of the interaction of annual precipitation and mean annual temperature on the means and variances of the traits in which the interaction term was the best predictor in the multiple regression (see Supplementary material Appendix 7, Table G1–2 for multiple regression results). The lines represent the effect of annual precipitation on the variable on y axis using the highest (red) and lowest (blue) bound of mean annual temperature. These plots were created in R using the library 'sjPlot'.

remained similar, although they became stronger and significant for non-standardized trait variances (Supplementary material Appendix 6, Table F1). All trait mean values except of standardized wood density correlated positively with the number of species (Table 2 and Supplementary material Appendix 6, Table F1).

Discussion

We found that more stressful (cold, arid, or seasonal) climatic conditions did not universally reduce trait variance within an assemblage. Furthermore, reduction in assemblage trait variance was often not associated with reduction in species richness. Instead, significant shifts in assemblage trait means driven by climate often strongly corresponded to the variation in number of species. Changes in selection pressures across environmental gradient responsible for variation in trait means are thus also important for species richness.

Shifts in mean trait values were strongly correlated with climate, in agreement 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 warm sites with sufficient water availability, corresponding to our prediction and to the trade-off between plant height and drought tolerance (Ryan et al. 2006, Moles et al. 2009). Woody species growing in hot, dry and cold conditions had a low specific leaf area, since small and thick cells are more tightly packed and can thereby reduce water or heat loss (Poorter et al. 2009).

The increase in seed mass with temperature correspond to our prediction that increase in competition intensity in more benign conditions leads to a higher investment in initial growth of individual seedlings (Moles and Westoby 2006). The increase in mean wood density with increasing precipitation seasonality and with temperature can be interpreted as an adaptation of dense wood against drought-induced embolism (Hacke et al. 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, the reduction in variance of specific leaf area 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 theirs 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, when using the evolutionary distinct species pools of tropical and temperate taxa, but not within the species pool of North America or North American vegetation ecoregions.

In contrast with our first and second prediction, variance in height and wood density decreased neither with increasing environmental harshness, nor with decreasing species richness. Instead, variances in values of these two traits were

lowest in climatically benign conditions, while high variances were typical for cold environment or the combination of warm and dry environment. This could be explained by 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 slowly growing trees with dense wood could be more disadvantaged (Adler et al. 2014), 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 (Supplementary material Appendix 8, Fig. H1). Competitive hierarchies can thus be an important factor shaping trait distributions in large-scale species assemblages (Mayfield and Levine 2010, Wisz et al. 2013, Araújo and Rozenfeld 2014), although we cannot directly test the effect of biotic interactions here. Unlike variance in height and wood density, variance in seed mass and specific leaf area increased with species richness, although the positive correlation between variance in specific leaf area and species richness was very weak and became weakly negative when using only angiosperm data. This indicates that seed mass may be important trait 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, Stahl et al. 2013, Hawkins et al. 2014). Nevertheless, given that the traits we used have been proposed 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 (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). Also, the quality of the trait values extracted from databases may be less biased for widespread (well-sampled) species than for rare species (Violle et al. 2014). Similarly, including intraspecific trait variation could potentially increase the evidence for significant filtering at the plot scale (Jung et al. 2010, Violle et al. 2012). Such data are, however, not available for large scales. Uneven distribution of species with known trait values can cause another bias as the proportion of the missing trait values is highest in extreme environment. Species from these habitats could be a good target for future measurements. It is also possible that trait values are constrained by other filters such as frequency and magnitude of fires or floods (Bond and Keeley 2005, Ojeda et al. 2005, Glenz et al. 2006). Also significant filtering could appear at finer spatial scale or the effect of environmental filtering could have been masked by biotic interactions. 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, Lamanna et al. 2014).

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.

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