

LETTER

Tree diversity, tree height and environmental harshness in eastern and western North America

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Abstract

Does variation in environmental harshness explain local and regional species diversity gradients? We hypothesise that for a given life form like trees, greater harshness leads to a smaller range of traits that are viable and thereby also to lower species diversity. On the basis of a strong dependence of maximum tree height on site productivity and other measures of site quality, we propose maximum tree height as an inverse measure of environmental harshness for trees. Our results show that tree species richness is strongly positively correlated with maximum tree height across multiple spatial scales in forests of both eastern and western North America. Maximum tree height co-varied with species richness along gradients from benign to harsh environmental conditions, which supports the hypothesis that harshness may be a general mechanism limiting local diversity and explaining diversity gradients within a biogeographic region.

Keywords

Alpha diversity, diversity gradients, environmental favourability, gamma diversity, harshness hypothesis, maximum tree height, site index, tree species richness.

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INTRODUCTION

An improved understanding of diversity patterns is a primary concern for ecologists, evolutionary biologists, biogeographers, palaeontologists and increasingly conservation scientists. Historical factors have been shown to play major roles in explaining variation in diversity among biogeographic realms (Latham & Ricklefs 1993), but explanations for geographic variation in diversity within realms have been less compelling. We suggest that within a biogeographic region, geographic variation in diversity for any given functional group may be best explained by spatial variation in the strengths of environmental factors that constrain the growth and survival of species in that functional group. We call the total effect of all such constraining variables environmental harshness, and hypothesise that it acts as an ecological and evolutionary filter on diversity. Harshness is intuitively appealing as an explanation because of its qualitative consistency with latitudinal diversity gradients, and was one of the first hypotheses proposed for such gradients (Whittaker 1965). Yet harshness has frequently been rejected as a useful basis for diversity theory because of difficulty in defining environmental harshness in a way that is easily measurable and is independent of species richness (Rohde 1992).

Many explanations for diversity gradients, in general, and latitudinal gradients in species richness, in particular, have been proposed (for a review, see e.g. Mittelbach *et al.* 2007). These hypotheses are not all mutually exclusive, as multiple mechanisms surely contribute, with different mechanisms dominating at different scales. Historical factors, such as the area a biome has had over evolutionary time, have been implicated as a dominant factor in explaining differences in diversity among biogeographic regions (e.g. Latham & Ricklefs 1993; Fine & Ree 2006). In contrast, geographic variation in

diversity within these regions is often strongly associated with current climate. For example, evapotranspiration, a correlate of productivity, is strongly correlated with tree species richness in North America (Currie & Paquin 1987). One climate-based mechanism could be that warmer temperatures are associated with, or perhaps cause higher speciation rates due to, higher mutation or evolutionary rates at higher temperatures (Rohde 1992; Allen *et al.* 2006). There have been few empirical tests of this hypothesis to date (e.g. Wright *et al.* 2006; Bromham *et al.* 2015), and none that distinguish whether higher evolutionary rates are caused directly by higher temperature. The fact that some diversity gradients are unrelated to temperature such as soil bacterial diversity which responds primarily to pH (Fierer & Jackson 2006), implies that the variation in species richness along contemporary environmental gradients within regions may require a more general explanation.

We argue that quantification of environmental harshness may provide an overarching explanation for geographic variation in diversity within a region for any particular functionally similar group of species, such as trees. Swenson *et al.* (2012) and Stahl *et al.* (2014) have shown that environmental harshness limits the range of species traits that are viable in trees. Kleidon & Mooney (2000) have proposed that harshness limits diversity by limiting the range of species traits that are viable. However, a test of this hypothesis requires an operational definition of harshness that allows it to be observed and measured in a way that is independent of diversity. It is well known that climate variables, such as the minimum temperature occurring in an area, and evapotranspiration, as well as soil fertility, and other environmental factors influence growth and mortality rates. However, although each of these factors contributes to harshness, no single environmental factor is a measure of harshness. We propose that harshness can

be defined operationally in terms of a measurable physiological or morphological trait that represents the integrated response of individuals to the full suite of the factors that contribute to harshness. We pursued this approach for tree species richness, and test its predictions for alpha diversity (local, within-site), beta diversity (turnover among sites) and gamma diversity (total diversity at larger spatial scales) in both eastern and western North America.

We propose that the maximum tree height observed among many mature adult individuals at a given site is a useful integrative indicator of the environmental suitability of that site for trees. Foresters call the maximum height attained by a given tree species at a given age the 'site index', which they use as a measure of site quality. A tree's height is critically important for its acquisition of light, and thus for its growth, survival, reproduction, competitive ability and fitness (King 1990). The relative harshness of environmental conditions places constraints on the maximum tree height (Givnish *et al.* 2014; Stahl *et al.* 2014). Higher salinity, high wind exposure, colder temperatures, shorter growing season, drought, nutrient deficiency and soil anoxia all reduce maximum tree stature. Mangroves, for example, experience multiple challenges: maintaining mechanical integrity on soft ground in the face of wind and wave exposure, and tolerating both high salinity and daily flooding. Mangrove forests are less species rich and of lower stature than nearby freshwater swamps, which in turn are less species rich and shorter than nearby upland forests (Beard 1955). Indeed, there are no mangrove forests at all in temperate climates with significant freezing stress (Keogh *et al.* 1999). For the tree life form, maximum height integrates the interacting effects of multiple environmental limiting factors into a single easily measured index of environmental harshness.

The total niche space that allows persistence of the tree life form can be conceived as a volume in multidimensional space, one of whose dimensions is height, with different species having different mature heights that could range from the smallest height defined as a tree, to the maximal height observed in an area (Westoby *et al.* 2002). Other axes of importance likely include differences in seed mass, leaf life span, wood density and so on (Westoby *et al.* 2002). Clearly, the larger the maximum tree height that is possible in an area, the larger would be the potential niche breadth along the mature height axis. Furthermore, we suggest that for other niche axes as well, the range of feasible possibilities in a site depends on the suitability of the site for trees in general, which is indicated by maximum tree height. If as a first approximation, we assume that a new species is more likely to form (speciate) within a region if its niche differs by at least a certain minimal amount from the niches of its competitors, then regions with less niche space (from greater harshness) should equilibrate at a lower tree diversity than those with greater niche space (Tilman 2004). This perspective assumes that multispecies coexistence is promoted by tradeoffs among these life history strategies, and predicts that tree species richness should be approximately proportional to niche volume in this multidimensional space and thus scale with tree height (Loehle 2000). Tradeoffs between competitiveness under benign conditions caused by greater height growth rates vs. traits that permit survival

under harsh conditions might also explain why many stress tolerant species are rare or absent from more benign habitats, thereby contributing to beta diversity (Loehle 1998; Koehler *et al.* 2012; Savage & Cavender-Bares 2013).

Apart from variation in the size of the tree niche space along harshness gradients, there may be asymmetries in extinction and colonisation if conditions vary over time, as they do in glacial cycles for example (Slobodkin & Sanders 1969). Specifically, if environmental conditions become harsher, species lacking the appropriate stress tolerance would be more likely to go extinct locally (and globally if migration to areas with appropriate climate was not possible), while other species that had sufficient stress tolerance would likely survive (Latham & Ricklefs 1993; Svenning 2003; Willis *et al.* 2007). When more benign conditions returned, the surviving species would quickly colonise less harsh habitats from which they are no longer excluded by competition from the now extinct species. By contrast, if there were empty niches on the harsh end of conditions, it would take substantial evolutionary change before species lacking stress tolerance could adapt to the harsher conditions and colonise (Ricklefs *et al.* 2006; Zanne *et al.* 2014). Indeed in trees, ancient lineages are associated with harsh environments (Page 2004) and few tropical lineages have expanded into temperate parts of North America (Fine 2001). Moreover, despite several hundred millions of years of evolution, no trees have evolved the ability to survive and reproduce in the extremely harsh conditions of high altitude and latitude, as evidenced by the existence of tree lines. Tree lines demonstrate that no species of trees can survive and reproduce beyond a certain coldness or harshness, conditions under which century old outlier trees may be only a metre tall (Wieser & Tausz 2007).

If these assumptions are a reasonable caricature of nature, one would expect that, within a biogeographic region, the maximum tree height at a site with a mature stand would be a strong correlate of alpha species richness at that site. Likewise, the height of the tallest trees in a given forested sampling site would be a reasonable predictor of alpha tree species richness, even though on some plots the trees will not yet be fully mature. Other measures of environmental harshness such as productivity, minimum temperatures and prevalence of shade, drought and soil water logging would also be good predictors of alpha tree species richness. Furthermore, maximum height and species richness would be expected to show similar, but less robust, responses to these components of harshness. Similarly, the maximum tree height occurring across all plots in a region would be a correlate of total regional species richness. The relationship between maximum height and richness should be stronger at the regional scale because this would decrease the effect of plots in which the tallest tree had not yet reached its full height. Finally, beta diversity is expected to be positively related to environmental heterogeneity among plots, as quantified by the range in measures of environmental harshness among plots. Our results show that tree height is indeed a consistent index of environmental harshness and a strong predictor of tree species richness in eastern and western North America, lending support to the environmental harshness hypothesis as an explanation of diversity gradients within regions.

METHODS

We investigated the empirical relationships among species richness, maximum tree height and multiple environmental stress measures using the Forest Inventory and Analysis (FIA) data gathered by the USDA Forest Service across a network of monitoring plots covering the lower 48 states of the USA (Forest Service U.S.D.A. 2008). We separately analysed data for two biogeographic regions: eastern North America and western North America (regions east and west of the Prairies). For our purposes, we have defined biogeographic regions as regions that have been sufficiently isolated from each other for long enough to have separate species pools (i.e. share few species), and that lack major internal barriers to species dispersal that could have inhibited species from reaching habitats where they could potentially survive and compete. Eastern and western North America forests meet these criteria for separate biogeographic regions (Tiffney & Manchester 2001; Donoghue & Smith 2004). Only 24 of the 348 species in the FIA data we used were common to both regions several of which are species introduced by people. We did not include Alaska in the final analysis because Alaska was disjunct from the rest of the region covered (preliminary analyses that included Alaska produced qualitatively and quantitatively similar results). We used the FIA data from the latest completed inventory cycle in each of the lower 48 conterminous United States as of February 24, 2015. The FIA data may be downloaded from the USDA Forest Service website (Forest Service U.S.D.A. 2015).

Each FIA plot has a total area of 672 m² and consists of four subplots arranged in a cluster, with one central plot and three peripheral plots spaced 120° apart in a 36.5-m radius circle around the central plot (Forest Service U.S.D.A. 2008). We included only data from plots in natural stands with at least eight trees per plot, for a total of 54 906 plots in eastern North America and 27 788 plots in western North America. Natural stands refer to plots that are forested (as defined by the FIA manual), and lacking any evidence of artificial regeneration (i.e. trees were not planted). Trees were defined as individuals which are 12.7 cm diameter or greater at breast height (dbh) and alive at the time of census. For each plot, we determined maximum tree height and (alpha) tree species richness. The FIA data also included plot productivity class (Forest Service U.S.D.A. 2008).

We compiled information from multiple sources to obtain various measures of environmental harshness for each plot. From the FIA data themselves we used plot productivity class, a measure of favourability (the opposite of harshness) (Forest Service U.S.D.A. 2008). As a measure of cold stress, we calculated plot-specific means of January minimum daily temperatures between 1981 and 2010 (PRISM Climate Group 2012). Using tree species composition combined with species tolerance values from a recent meta-analysis (Niinemets & Valladares 2006), we calculated the abundance-weighted average shade tolerance, average drought tolerance and average soil water logging tolerance for each plot. We note that each of these quantities has limitations as a measure of harshness, and should be taken as at best an imperfect indicator of one or more stresses. For example, the species tolerance values are

imperfect measures of the underlying true species environmental tolerances, and plot averages of these are indirect and even more imperfect measures of associated environmental stresses.

We analysed the among-plot relationships of alpha species richness with each of the other variables by first fitting a cubic spline for alpha species richness as a function of the independent variable and then calculating Pearson correlation coefficients between fitted and observed plot-level values, with separate analyses for eastern North America and western North America. We similarly analysed the relationship of maximum height with productivity and other measures of harshness, and of productivity to the remaining measures of harshness. All cubic splines were fitted using the 'smooth.spline' function in the statistical software R using the default settings for that function (number of knots = number of data points^{0.2}; and knots are evenly spaced). More generally, all statistical analyses and graphs were done in R, version 3.0.2 (R Core Team 2013).

To analyse gamma (regional) scale values, we aggregated data into grid cells by converting plot latitude and longitude to an Albers equal area conic projection with the standard parallels used by the USGS (Snyder 1982), and assigned plots to grid cells with dimensions of 100 × 100 km². For each grid cell, we calculated gamma species richness and average alpha species richness, as well as minimum, mean, maximum and range in the explanatory variables from plot data. To avoid bias due to regional differences in sampling intensity in the FIA data, grid cell values were calculated by taking the mean of 1000 repeat samples of 100 plots from each grid cell, including only cells with over 100 plots (230 grid cells in eastern North America, 116 in western North America). Sampling was done without replacement (i.e. each sample of 100 plots did not include any plots more than once). Within each region, we analysed the bivariate relationships of grid cell mean alpha species richness with grid cell means of maximum height and other measures of harshness like minimum January temperature by fitting separate cubic splines for each case, and then calculating Pearson correlation coefficients (*r* values) between the fitted and observed richness values. We similarly analysed the relationships of gamma species richness with grid cell extreme favourable values of harshness measures (i.e. maxima of max height, productivity class and minimum January temperature, and minima of shade tolerance, drought tolerance and water logging tolerance).

For each grid cell, we calculated beta species richness by dividing gamma by average alpha species richness (Whittaker 1965). We then analysed the relationship of beta species richness with the grid cell ranges of maximum height, productivity and other measures of harshness, using cubic splines and Pearson correlation coefficients as above. Note that range and maxima are highly correlated for most of these variables.

We tested various alternative methods to assess the robustness of our results. For example, we tried including all plots in grid cells, or including all grid cells regardless of number of plots, or using a different minimum tree number per plot for plot inclusion in the analyses. These variations led to only slight changes in *r* values, leaving the qualitative results entirely the same, and thus we report only the main results here.

RESULTS

Within each region, alpha (plot level) tree species richness was highly significantly associated with plot maximum tree height (Fig. 1). Consistent with the harshness hypothesis, productivity, January mean of minimum daily temperatures as well as average plot shade, drought and water logging tolerance also were correlated with alpha species richness (Fig. 1). These relationships become stronger when using the $100 \times 100 \text{ km}^2$ grid cell mean of plot species richness and environmental variables (Fig. 2). Species richness was a monotonically increasing function of maximum height and productivity, with a stronger relationship for height than for productivity. In contrast, alpha species richness sometimes showed a hump-shaped response to minimum January temperature, mean shade tolerance, mean drought tolerance and mean water logging tolerance (Figs 1 and 2). In general, maximum tree height and tree richness were similarly related to environmental variables in qualitatively similar ways as richness (Fig. 1). In eastern North America, maximum height had the highest explanatory power for richness of any variable examined; in western North America, unimodal relationships with shade tolerance and water logging tolerance were slightly better predictors. If analyses allowed only linear or monotonic relationships, then maximum height would always be the strongest predictor of alpha tree species richness.

In both regions, gamma species richness increased strongly and almost linearly with maximum tree height (Fig. 3). Grid cells with harsher environments as indicated by lower productivity, colder winter temperatures, shade, drought or water logging had lower gamma species richness (Fig. 3). Grid cell maximum height showed very similar responses to environmental variation as did gamma species richness (Fig. 3). In both regions, the maximum of maximum height was the second-best predictor of gamma species richness, after the maximum of January minimum temperature (Fig. 3).

Beta diversity was strongly related to ranges of various harshness measures. It was especially well predicted by range in drought tolerance and range in maximum tree height (Fig. 4). Overall, species richness was greater in eastern North America than in the drier western North America (Table 1), as is also evident in all figures comparing the two.

DISCUSSION

The results for both regions support our hypotheses that, within biogeographic regions, benign environments have greater species richness than harsher environments, and that maximum tree height serves as an indicator of environmental favourability for trees. Maximum tree height consistently explains the variation in both alpha and gamma diversity as indicated by the monotonic relationships in Figs 2 and 3.

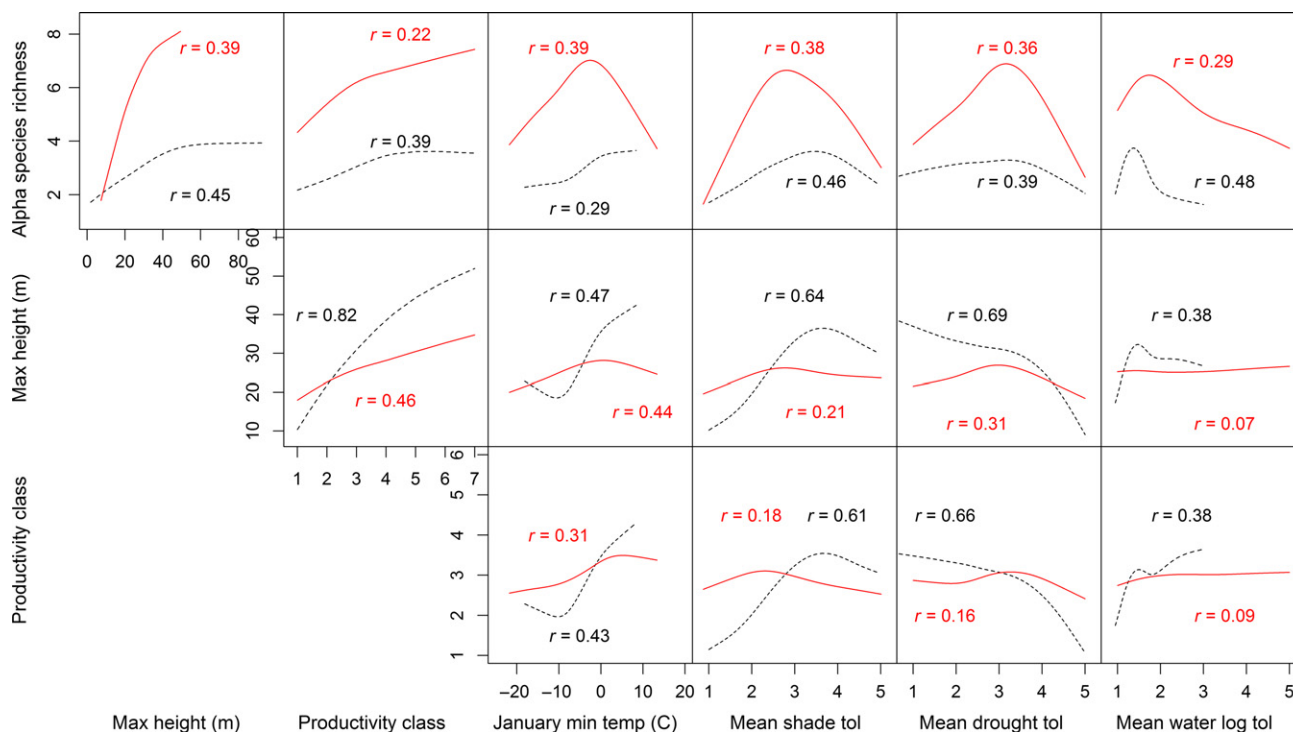


Figure 1 Variation in alpha tree species richness among forest inventory plots in both eastern North America (red solid) and western North America (black dotted) is explained in part by measures of environmental harshness: maximum tree height, productivity class, maximum tree diameter, mean of the January daily minimum temperature, mean shade tolerance, mean drought tolerance and mean soil water-logging tolerance of the trees. Alpha species richness and maximum tree height show qualitatively similar relationships with the other measures of environmental harshness, relationships shared with a lesser degree by productivity. Lines are cubic splines with associated Pearson correlation coefficients, r . FIA productivity classes estimate the potential for sites to produce wood in $\text{m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ based on mean basal area increment, and are as follows: 1 = 0–1.39, 2 = 1.40–3.50, 3 = 3.50–5.94, 4 = 5.95–8.39, 5 = 8.40–11.54, 6 = 11.55–15.73, 7 \geq 15.74. See FIA manual for details (Forest Service U.S.D.A. 2008). Dots for individual plots not shown because of the large number of field plots.

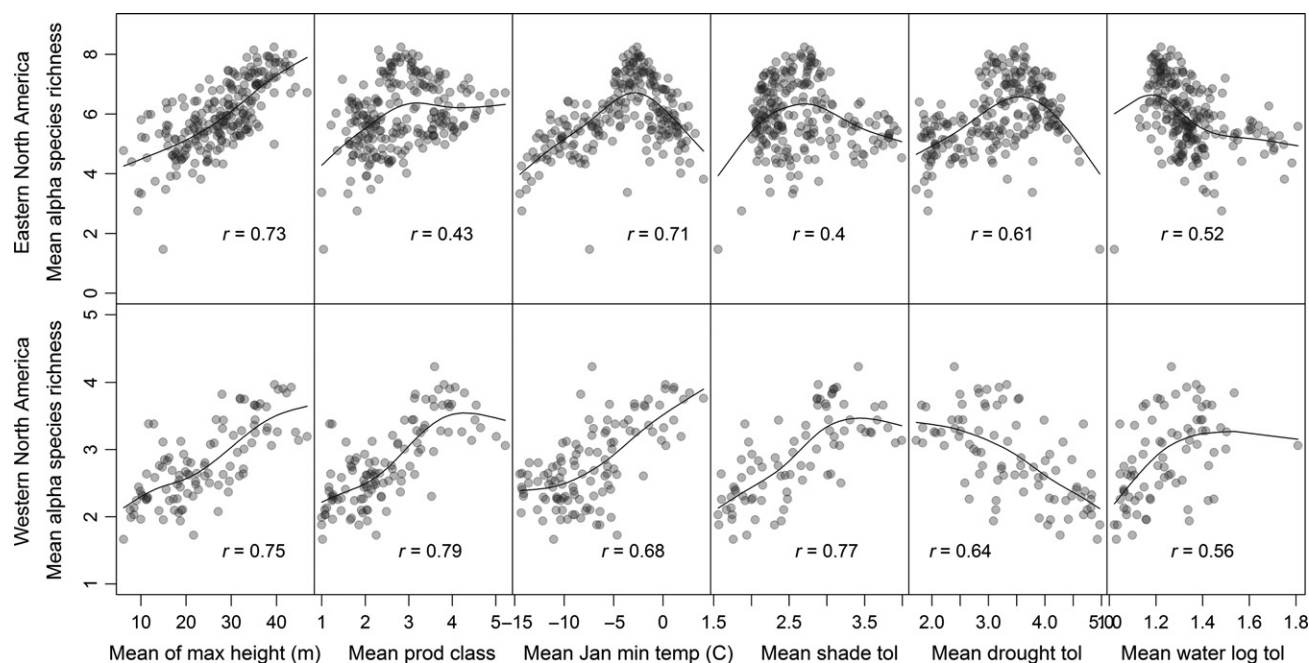


Figure 2 Variation among $100 \times 100 \text{ km}^2$ grid cells in mean alpha tree species richness in both eastern North America (upper panels) and western North America (lower panels) is strongly explained by environmental harshness, specifically grid cell means of the following: maximum tree height, productivity class, January mean of the daily minimum temperature and plot mean shade tolerance, drought tolerance, and soil water-logging tolerance. Lines are cubic splines with associated Pearson correlation coefficients, r . Each dot represents one grid cell. See Fig. 1 for productivity classes.

Indeed, the relationships between maximum height and average alpha and gamma diversity shown in Figs 2 and 3 are as tight as any reported in the diversity gradients literature (e.g. Currie 1991), although correlation coefficients are not directly comparable because of differences between studies in the geographic scale of analysis. The correlations are less strong at the plot scale (Fig. 1), as would be expected given that not all plots have mature trees to provide an accurate estimate of the potential maximum tree height. This measurement error is reduced when looking at patterns at the grid cell scale, which are therefore much stronger (Figs 2 and 3).

Overall when examining results at local and landscape scales, tree height was the best predictor of tree species richness, integrating effects of multiple stressors whose relative importance varied with scale. At the local plot scale, shade tolerance and water logging tolerance were slightly better predictors in western North America, but only because our spline-based analysis allowed hump-shaped (i.e. unimodal) relationships. If we had restricted the analysis to monotonic relationships, maximum tree height would have been the strongest predictor by far. Tree height remained the better predictor in eastern North America and at grid cell scales. At the grid cell scale, minimum January temperature was a slightly better (and monotonic) predictor of richness than was height, consistent with the importance of species cold hardiness in determining range limits (Loehle 1998; Koehler *et al.* 2012), but it had clearly lower explanatory power at local scales. At both plot and grid cell scales, the response of species richness to individual measures of harshness took the same form as the response of maximum height to these measures, even as the relationships changed with scale. In

particular, height echoes the hump-shaped responses of richness to shade, drought and waterlogged soils at the alpha scale. These hump-shaped relationships are to be expected given that droughty sites tend to have little water logging and vice versa, and similarly dry sites are unable to support sufficient foliage to create deep shade. The strength of investigating tree species richness gradients through the lens of maximum tree height lies in this consistency for height to respond in parallel to richness on multiple environmental gradients including at the more difficult to predict smaller spatial scales.

The relationships with minimum January temperature, in particular, nicely illustrate the strengths of tree height as an integrative measure. At the plot scale, species richness shows an anomalous decline at the mildest temperatures in eastern North America. Notably, maximum height also declines in this temperature range in eastern North America, and thus maintains a monotonic relationship with richness (Fig. 1). At the grid cell scale, species richness and maximum height both plateau with respect to minimum temperature in the same temperature range in eastern North America, and again maintain a monotonic relationship with each other (Fig. 3a). An examination of the data suggests that the anomalous decline in both species richness and maximum tree height at the mildest winter temperatures in eastern North America is at least in part due to increases in water logging in southern Florida, a landscape dominated by the vast Everglades wetlands (results not shown). Flooding and soil water logging cause anoxia in the root zone which inhibits tree growth and thus reduces height (crown dieback is a common symptom of flood stressed trees). Long duration soil anoxia can cause tree mortality,

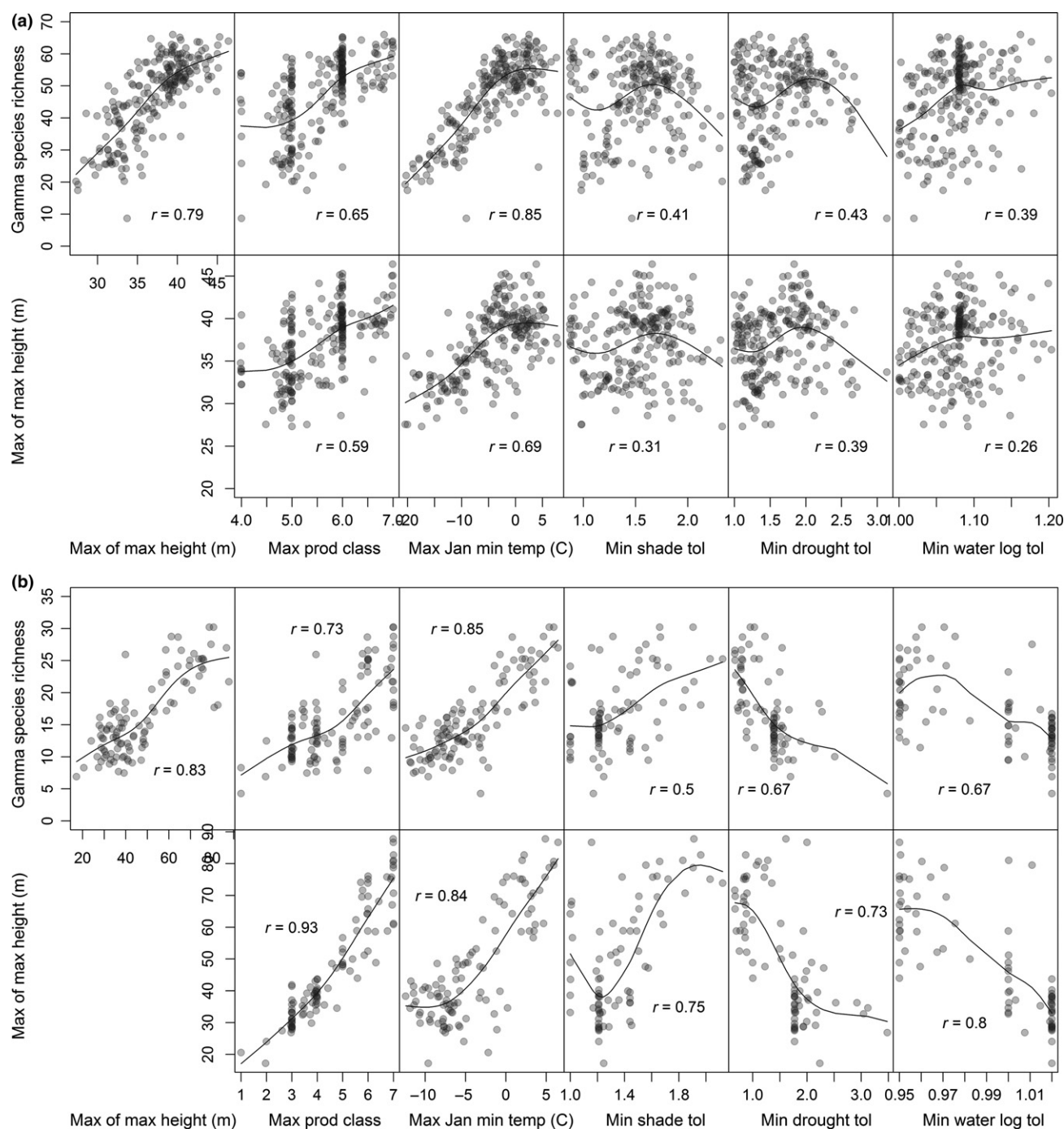


Figure 3 Variation in total species richness among $100 \times 100 \text{ km}^2$ grid cells in eastern North America (A) and western North America (B) is strongly explained by environmental harshness as quantified by the following: maxima of tree height, productivity class, and January mean of the daily minimum temperature and minima of plot mean shade tolerance, drought tolerance and soil water-logging tolerance. Maximum tree height shows a qualitatively similar response. Lines are cubic splines with associated Pearson correlation coefficients, r . Each dot represents one grid cell. See Fig. 2 for productivity classes.

especially in seedlings of species lacking appropriate adaptations to cope with a lack of oxygen, and hence acts as an ecological filter reducing species richness. The strong seasonality of precipitation in Florida can bring additional stresses like drought and fire. In other words although conditions are becoming less harsh with respect to temperature in southern Florida, they are becoming harsher with respect to other

conditions. Regardless of the explanation for this specific geographic pattern, it is clear that maximum height as a predictor of tree species richness appears to be robust to the idiosyncrasies of the geography of a particular region.

As would be expected, beta diversity was well predicted by the range in stress measures, especially the range in maximum tree height and the range in drought tolerance (Fig. 3). This

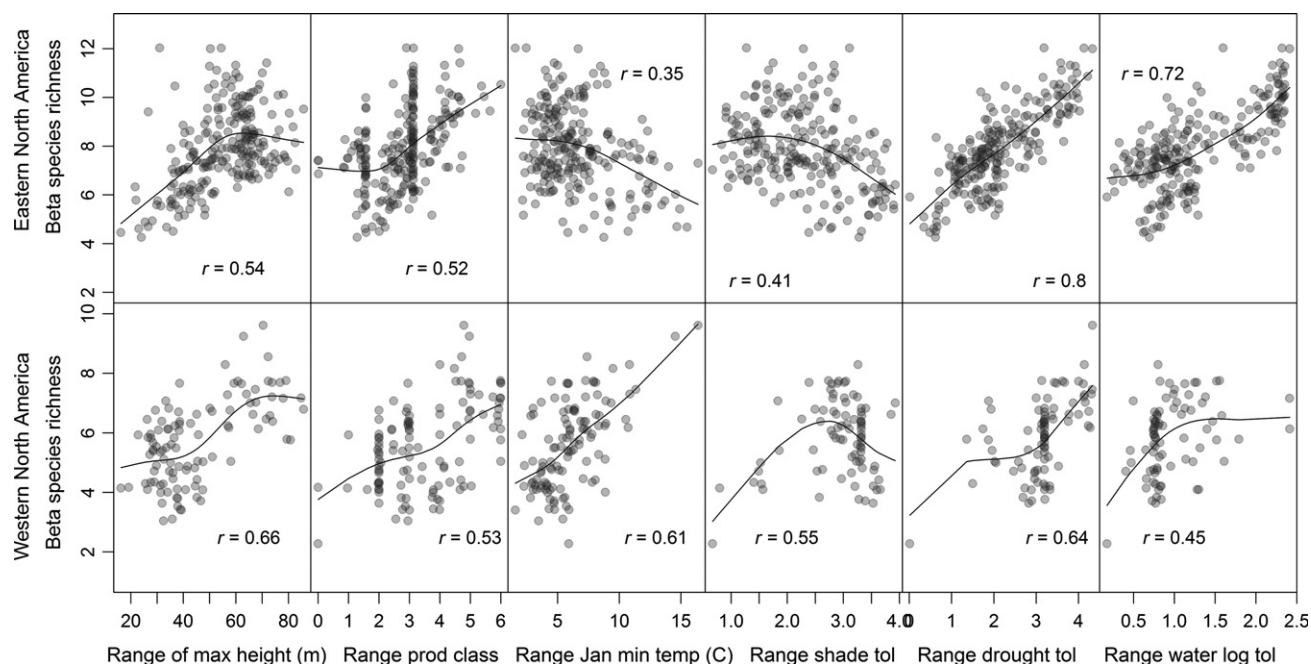


Figure 4 Variation among $100 \times 100 \text{ km}^2$ grid cells in beta species richness (species turnover among plots) in both eastern North America (upper panels) and western North America (lower panels) is strongly related to ranges of environmental harshness variables within grid cells: specifically, ranges of maximum tree height, productivity class, January mean of the daily minimum temperature and mean shade tolerance, drought tolerance and soil water-logging tolerance of the trees on the plot. Lines are cubic splines, with associated Pearson correlation coefficients, r . Each dot represents one grid cell. See Fig. 2 for productivity classes.

Table 1 Tree species richness statistics from the Forest Inventory Analysis data for the eastern and western coterminous United States, here referred to as eastern North America and western North America respectively

Tree species richness	Eastern North America	Western North America
Mean alpha	5.8	2.7
Mean beta	7.9	5.6
Mean gamma	46.9	15.8
Region total	237	135

result confirms the well-established importance of soil moisture gradients to tree species distributions and thus also beta diversity in both eastern North America (Curtis & McIntosh 1951; Whittaker 1956) and western North America (Waring & Major 1964; Whittaker & Niering 1964). This turnover in tree species along moisture gradients has been shown to be related to species physiological traits in both temperate (Cavender-Bares *et al.* 2004) and tropical forests (Engelbrecht *et al.* 2007) consistent with our hypothesis.

These data suggest a potential hierarchy of stress gradients. Temperate tree species diversity at the largest scale examined here (gamma) is most strongly related to minimum winter temperatures, species turnover within regions (beta) is most strongly related to soil moisture and richness at the local plot scale (alpha) is most strongly related to maximum tree height, which integrates the effects of multiple stresses. These results are consistent with the intuitively appealing idea that, at increasingly small spatial scales, many different types of environmental stresses act simultaneously, causing local species

richness to depend on the cumulative effect of these multiple ecological filters as embodied in maximum tree height.

Results in the two biogeographic regions were qualitatively similar, but with some substantial quantitative differences: eastern North America had a larger species pool and higher species richness at all scales (Table 1), while western North America had greater tree heights (Fig. 1). Given the strength of these regional differences, the strong positive relationships between height and tree species richness observed within regions are obscured when data for the two regions are combined. Differences in the size of the tree species pool among biogeographic regions can be explained by geologic history and its influences on past and present area under similar climatic conditions (Latham & Ricklefs 1993; Fine & Ree 2006). Western North America once supported species rich mesophytic deciduous broadleaf forests dominated by Angiosperm tree species similar to the deciduous forest species that survive in eastern North America and eastern Asia. These mesic and hydric deciduous species disappeared from western North America during the tertiary, a time of climatic drying and orographic change in western North America (Tiffney & Manchester 2001; Donoghue & Smith 2004). Despite this loss of mesic species in western North America, its species richness today is still greater in taller, more mesic forests. This pattern suggests that within biogeographic regions there is a deterministic process of ecological sorting and/or evolutionary change that creates species richness distributions which are positively correlated with environmental favourability and maximum tree height in spite of the vicissitudes of geologic history.

The strength of evidence supporting the environmental harshness hypothesis of species diversity gradients in North American trees suggests that it merits more research in future. An obvious next step would be to investigate if there are consistent relationships between tree height and richness, and environmental harshness in other parts of the world. Similarly, can analogues to height in trees as an integrated measure of harshness be found for other life forms? Given that historical factors clearly play a role in explaining diversity differences among biogeographic regions, it would be interesting to see whether they sometimes are sufficiently important as to overcome the expected harshness induced patterns within regions, for example in Europe where recent glacial cycles have caused more tree species extinctions than in East Asia or North America (Svenning 2003). Another important future direction is investigating the mechanisms that could contribute to diversity variation on harshness gradients, in particular the potential roles of ecological sorting, evolutionary change and net diversification. We have suggested that more benign environments permit a broader range in heights and other traits resulting in more niches favouring coexistence of more species. This hypothesis could be tested with forest stand simulation models for different types of forests within a region. Investigation of life history tradeoffs related to mature tree height and height growth rate could further elucidate the underlying mechanisms. We also proposed that there is an asymmetry with respect to colonisation. Specifically, stress tolerant lineages can easily colonise unoccupied niches in benign environments, whereas lineages from benign environments would first need to evolve traits permitting growth and survival under stressful conditions before they could colonise harsh environments. Since adaptation to more stressful conditions is a slow process, we expect diversification rates to be higher in benign environments (as indicated by greater mature tree heights and height growth rates), a hypothesis that could be investigated with phylogenetic methods.

Our findings suggest that maximum tree height is an effective integrator of the effects of environmental harshness, and that harshness limits diversity. Maximum height is a single easily measured trait that is a surprisingly strong predictor of tree species richness. As such it has the potential to help with conservation planning which is increasingly based on models because actual species data are often lacking at the spatial resolution of individual land parcels. Proxy data layers available as model inputs in GIS (geographic information systems) such as elevation, geology and climate have been used to insure inclusion of beta diversity in conservation priority area maps (e.g. Anderson & Ferree 2010), but complementary approaches to identify individual land parcels with relatively high alpha diversity within a region are not as well developed. Forests with high alpha diversity are of conservation importance because remaining forest patches in anthropogenic landscapes in general and protected forests in particular are disproportionately shorter stands located in harsher less productive environments (Sanderson *et al.* 2015), which tend to also have lower alpha species richness, as we showed. Tree canopy height can be easily mapped over large areas at high spatial resolution with LiDAR (e.g. Lefsky 2010), and could help identify forest parcels with potentially high alpha species

richness. Descriptions of forests in other biogeographic regions suggest that empirical studies within these regions will also reveal a monotonic relationship between maximum tree height and tree species richness (e.g. Beard 1955). The generality of harshness gradients limiting both tree height and species richness implies that an improved understanding of the physiological and life history tradeoffs between coping with stressful environments and maximising tree height could also make important contributions to developing an improved understanding of how communities of forest trees are assembled and gradients in tree species richness emerge.

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AUTHORSHIP

CM originated the idea for the study in discussion with HM and DT. CM performed the analyses and wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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