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E-ARTICLE

# Constancy in Functional Space across a Species Richness Anomaly

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ABSTRACT: The relationship between large-scale gradients in species richness and functional diversity provides important information regarding the mechanisms driving patterns of biodiversity. A classic hypothesis in ecology is that strong interspecific interactions should result in an increase in the functional volume of assemblages as the species richness increases, whereas climatic constraints may result in no change in functional volume. Most research of this kind examines latitudinal gradients in species richness, but the results are likely confounded by underlying gradients in climate and phylogenetic composition. We take an alternative approach that examines functional richness across a tree species richness anomaly where species richness doubles from Europe to eastern North America. The results demonstrate that the functional richness on both continents saturates at a similar point as species richness increases and that the packing of functional space becomes tighter. Further, the species richness anomaly is driven primarily by genera unique to North America, but those genera contribute less than expected functional richness to the region, indicating a high level of redundancy with genera shared between the continents. Taken together, the results indicate that the species richness anomaly is associated with diversification within a climatically constrained trait space. More generally, the work demonstrates the power of utilizing species richness anomalies in biodiversity research, particularly when they are coupled with information regarding organismal function.

*Keywords*: diversity anomaly, functional diversity, functional traits, species richness, temperate trees, trait space.

## Introduction

Gradients in species diversity are ultimately the result of differential speciation, extinction, immigration, and extinction rates through space and time (Mittelbach et al. 2007; Swenson 2011). The spatial distribution of functional diversity may provide a key to unraveling the relative contribution of these mechanisms in producing regional-scale species diversity and how this influences local-scale diversity (Swenson and Enquist 2007; Swenson et al. 2012). For example, a classic question in ecology has been whether strong interspecific interactions and limiting similarity (MacArthur and Levins 1967) result in a greater range of phenotypic space being occupied as species richness increases (Ricklefs and O'Rourke 1975; Ricklefs and Travis 1980). Alternatively, abiotic constraints on the amount of possible phenotypic space could give rise to a saturation in phenotypic space as species richness increases (Ricklefs 2009). Although there have been more and more studies quantifying the spatial distribution of functional diversity in relation to species richness along latitudinal gradients, the patterns can be difficult to interpret due to the large number of covarying factors. Specifically, there are large changes in climate and, perhaps more importantly, substantial changes in the phylogenetic composition along latitudinal gradients. This makes it unclear whether the change in functional diversity or the range in phenotypes is related to species diversity per se. Here, we implement a more powerful approach to studying the relationship between species diversity and functional diversity in the context of a species richness anomaly.

Species richness anomalies are powerful natural experiments where one can compare assemblages differing in species richness living in similar climatic conditions. Thus, species richness anomalies allow one to compare the differences in processes such as regional net-diversification rates (Dynesius and Jansson 2000; Ricklefs 2004; Kissling et al. 2012*a*) and test hypotheses such as limiting similarity as it relates to species richness gradients while reducing biases due to large changes in climate and phylogenetic composition. Perhaps one of the best-known species richness anomalies concerns the tree floras in the four main Northern Hemisphere temperate forest regions, where tree species richness is higher in East Asia than in eastern North America, which is again higher than in Europe and western North America (Latham and Ricklefs 1993*a*, 1993*b*; Ricklefs and Latham 1999; Ricklefs et al. 2004; Qian et al. 2005). The differences in species

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richness across regions have been ascribed to greater topographic heterogeneity, thereby promoting speciation rates via allopatry and greater tropical-to-temperate connectivity, thereby reducing extinction rates (Latham and Ricklefs 1993*a*, 1993*b*; Ricklefs and Latham 1999; Ricklefs et al. 2004; Qian et al. 2005). Notably, in Europe, it has been shown that the Pleistocene glaciations have caused a strong sorting of the regional assemblage of species and genera according to climatic tolerances (Svenning 2003).

Temperate tree species-diversity anomalies are also powerful for two additional reasons. First, there are many genera shared between the regions (Latham and Ricklefs 1993*a*; Wen 1999), making it possible to directly compare genera and thereby control changes in the phylogenetic composition across the richness gradient. Second, the genera unique to one region allow one to quantify the impact of differential speciation and extinction on regional-scale functional diversity. Specifically, one may ask whether the genera found in eastern North America and not Europe, either due to lack of dispersal or extinction of these lineages in Europe, disproportionately contributes to the functional diversity of the eastern United States.

In this study, we take advantage of the eastern North American–European tree species richness anomaly to investigate the relationship between regional-scale species richness and functional diversity. We first ask whether the functional diversity of regional-scale assemblages on both continents saturates as species richness increases, as would be expected if there are climatic constraints on niche volumes, or whether functional diversity continues to increase with species diversity, as would be expected under limiting similarity theory (MacArthur and Levins 1967; Ricklefs and O'Rourke 1975). Our second and related question is whether species pack more tightly into functional space as regional species diversity increases, as might be expected from a climatically constrained phenotypic space and/or finer partitioning of functional space, or whether the degree of packing into functional space is consistent with increases in species diversity, as would be expected under limiting similarity (MacArthur and Levins 1967; Ricklefs and O'Rourke 1975). Third, we exploit the ability to compare the species richness and functional diversity of the genera shared between the two regions to ask whether particular genera occupy a greater amount of functional space in eastern North America than in Europe, thereby permitting a greater number of species to regionally co-occur. Last, we quantify the relative contribution of shared genera and genera unique to each continent to the overall species richness and functional diversity on each continent, asking whether those genera that have arisen in only one continent or have gone extinct in one continent and not the other occupy distinctive functional space (Campbell 1982). For example, are those genera that are found only in eastern North America and not Europe functionally distinctive, thereby adding a disproportionate amount to the regional-scale functional diversity in the eastern United States?

## Methods

### *Geographic Data*

Geographic range maps for eastern North American and European tree species were used in this study. We defined "tree" in our study as any freestanding woody plant with a maximum height greater than 10 m. Tree species in these two regions that did not have trait data available in the literature for all traits were not included in the study. This ultimately resulted in 272 species in eastern North America and 117 species in Europe being analyzed in our study, which excludes a very small minority of the tree flora in each region. The eastern North American tree range maps were downloaded from the US Geological Survey (http://esp.cr.usgs.gov/data/little). The European tree range data were digitized from the European Floristic Atlas (http://www.luomus.fi/english/botany/afe). Both map data sets were regridded to 25 × 25-km, 50 × 50-km, and 250 × 250-km map grid cells, allowing us to repeat the analyses across scales.

### *Trait Data*

Our study utilized data for four traits that indicate where a species falls along spectra of plant ecological strategies. The first trait we quantified was the maximum height. This trait is related to the adult light niche of species, the ability to tolerate xeric environments, and recruitment (King et al. 2006; Moles et al. 2009). The second trait we quantified was seed mass. Seed mass is related to the regeneration niche of species (Grubb 1977) and represents a fundamental trade-off between producing many small seeds and few large seeds (Venable 1996). The third trait we measured was wood density. Wood density is often the best predictor of growth and mortality rates in tree data sets and represents a trade-off between rapid volumetric growth and mechanical instability versus slow volumetric growth and mechanical stability (on the tissue and organismal scale; Chave et al. 2009). The last trait we measured was leaf size. Leaf size is related to the area deployed for resource capture for a single leaf, but it is not necessarily related to overall canopy leaf area and leaf packing. Leaf size is also related to broadscale climatic gradients, given its interaction with leaf boundary layer thickness (Dolph and Dilcher 1980).

The trait data for our study were primarily collected from the literature but were supplemented through field collection of additional trait values by N. G. Swenson and the measurement of traits on herbarium vouchers. The maximum height data came from the literature where we recorded the absolute largest value reported (http://www

.americanforests.org/bigtrees) and the US Department of Agriculture PLANTS database (http://www.plants.usda.gov). The wood density data came from the global wood density database published by Chave et al. (2009) and additional literature sources (Swenson and Weiser 2010). Leaf area was estimated as the product of the reported leaf length, leaf width, and 0.70. This calculation has recently been shown to produce values highly correlated with the known area of leaves (Kraft et al. 2008) and represents a pragmatic approach for estimating leaf area for hundreds of species from the literature. For many species, the leaf length and/or width was not available in the literature and was recorded by Swenson using herbarium specimens in the Gray Herbarium at Harvard University and the Michigan State University Herbarium. Seed mass was recorded from the Kew Millennium Seed Database (http://www.data.kew.org/sid) and the PLANTS database. An additional 15 species had their seed masses quantified using seeds stored with herbaria sheets at the Michigan State University Herbarium by Swenson.

### *Analyses*

Our study quantified two measures designed to reflect the volume and packing of multivariate trait space. The volume of the trait space, which we refer to as the functional richness (Laliberte and Legendre 2010), was quantified as the volume of a convex hull. The functional richness was calculated using the R package FD and the dbFD function. Because trait data sets often have strongly covarying traits, this function reduces the data set using principal coordinate analyses. In our study, only the first two principal coordinate axes were retained by the program for the volume calculation. These first two axes were then used to calculate our metric of trait packing, the mean nearest neighbor distance. The mean nearest neighbor distance was simply the average Euclidean distance between a species and its closest neighbor in the two-dimensional principal coordinate space (Swenson 2014). We calculated the functional richness and the inverse of the mean nearest neighbor distance in the map grid cells and plotted the values against species richness. This was repeated across all three spatial scales. Next, a nonlinear regression function, Michaelis-Menten, was fit to the data using the drm function in the drc R package to test for significant asymptotic relationships. Last, because we were interested in whether functional space (i.e., functional richness) saturates with increasing species richness or linearly increases, we fit a linear model to the functional richness–species richness relationships and compared it to the Michaelis-Menten fit using the Akaike information criterion (AIC).

Next, we quantified the degree to which the functional similarity of grid cells on two continents is related to their climatic similarity. To accomplish this, we calculated the mean nearest neighbor distance between the species in each of the eastern North American map grid cells and each of the European map grid cells. Then, we used the WorldClim 2.5-min-resolution bioclimatic maps (http://www.worldclim.org) to extract values for each map grid cell for the 19 bioclimatic variables and altitude. The climate data were then scaled and used in a principal component analysis to limit data redundancy. The first nine principal component axes explained >99% of the variation in the data and were used to quantify a climatic dissimilarity matrix between all map grid cells. A Mantel test was then used to quantify the relationship between the functional dissimilarity and the climatic dissimilarity.

Next, we calculated the species richness and functional richness for 16 genera that are shared between the two data sets that contained two or more species. Shared genera that had less than two species per data set were excluded because a multivariate trait volume could not be calculated. A paired *t*-test was then used to quantify whether the species or the functional richness for the species in a genus in one data set was higher or lower than that for the species in the same genus in the second data set.

Last, we quantified the percent of the total species in each data set that were from genera shared between the two data sets or from genera not shared between the two data sets. We performed a similar calculation for functional richness, where we quantified the percent of the total functional richness in one data set covered by species from the shared genera and that covered by species from genera unique to a single data set. The percent contributions for species richness were then used to set the expected percent contributions for functional richness in a $\chi^2$ goodness-of-fit test for each data set.

## Results

We quantified the multivariate functional volume, hereafter referred to as the functional richness, of tree assemblages in 25 × 25-km, 50 × 50-km, and 250 × 250-km map grid cells in eastern North America and Europe (figs. 1, A1, A2). The packing of species into the observed functional volume was determined by calculating the mean nearest neighbor distance in multivariate space between species in a map grid cell (figs. 1, A1, A2). The nonlinear Michaelis-Menten asymptotic regression model was significant for all functional richness–species richness relationships across scales and continents and for all 1/mean nearest neighbor distance–species richness relationships across scales and continents (figs. 1, A1, A2). This indicated that each of the relationships were significantly asymptotic. We also fit linear regression models to each of the functional richness–species richness relationships to determine whether an asymptotic (i.e., saturating) function or a linear function provided a better fit by comparing AIC values. Across scales and continents, the asymp-

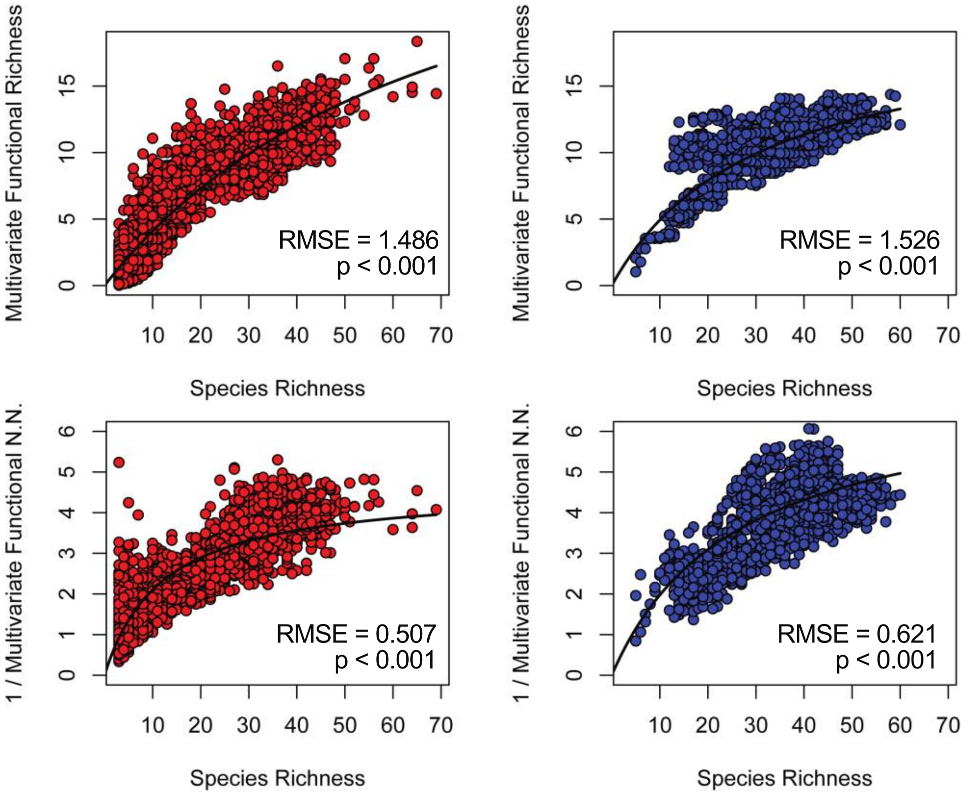

**Figure 1:** Relationship between volume and packing of trait space with tree species richness in 50 × 50-km map grid cells in eastern North America (red) and Europe (blue), fit with a Michaelis-Menten model. The top row plots the multivariate functional richness (i.e., the multivariate trait volume) against the species richness. The bottom row plots the inverse of the mean nearest neighbor (N.N.) distance in multivariate trait space between species in a map grid cell. The $P$ value is from the significance test of the asymptotic parameter in the Michaelis-Menten model. RMSE = root mean square error.

totic Michaelis-Menten model had stronger fits to the data than the linear model (table A1).

A Mantel test was utilized to compare the functional dissimilarity and climatic dissimilarity between map grid cells on the two continents. The functional dissimilarity was quantified using a mean nearest trait neighbor distance between species in separate grid cells. At each of the three spatial scales, there was a positive relationship (25 km × 25 km: $r = 0.21$, $P < .01$; 50 km × 50 km: $r = 0.19$, $P < .01$; 250 km × 250 km: $r = 0.22$, $P < .01$), demonstrating that map grid cells in similar climates have similar functional compositions.

A total of 16 genera containing two or more species were shared between the two regions. Paired $t$-tests were used to quantify whether the observed species richness or functional richness for species in each genus in one data set were higher or lower than in the other data set. No significant difference was found in the number of species per genus for the 16 shared genera in the two data sets ($t = -1.5119$, df = 15, $P = .1513$; fig. 2). The only genus that had a large species richness anomaly was *Quercus*, with more than double the number of species in the eastern North American data set than in the European data set. Similarly, we found no significant difference in the functional richness of species in each genus in one data set from the functional richness of the species in the same genus in the other data set ($t = -1.0815$, df = 15, $P = .2965$; fig. 3). Again, *Quercus* was the only genus with a major difference, with a much higher functional richness for this genus in eastern North America than in Europe.

The last set of analyses first quantified the percent of the total species richness in eastern North America and Europe that was contributed by species from genera shared between the two data sets and from genera unique to one data set. In eastern North America, 47.4% of the total tree species richness was contributed by species from genera not in the European data set, and 52.6% was contributed by genera shared between the data sets. In Europe, only 11.1% of the species richness was contributed by species from genera unique to the European data set, and 88.9% was contributed by shared genera. This difference in the relative contribution to regional species richness from unique genera was

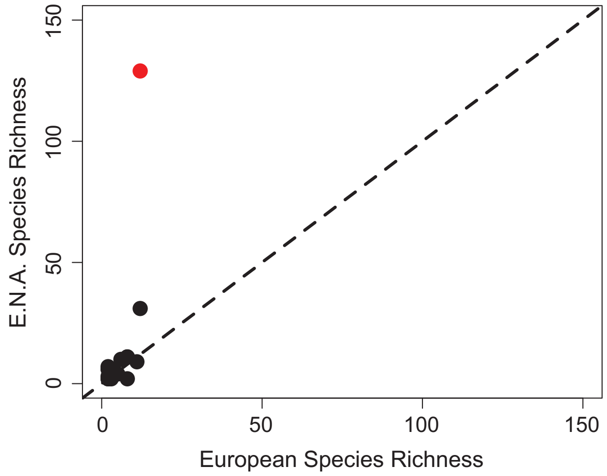

**Figure 2:** A total of 16 genera with two or more species were shared between the eastern North American (E.N.A.) and European tree data sets. The species richness within each of these genera in the eastern North American data set is plotted against the species richness for those genera in the European data set (black circles). The genus with the largest deviation was *Quercus*. A paired *t*-test found no difference between the species richness within genera between the two data sets ($t = -1.5119$, df $= 15$, $P = .1513$). The red circle indicates the total species richness for species from genera unique to the eastern North American data set plotted against the total species richness for species from genera unique to the European data set. The dashed line is the 1 : 1 line.

significant ($\chi^2 = 61.7972$, df $= 1$, $P < .001$; fig. 4). In other words, the species richness anomaly in this data set is largely explained by differences in the number of species in genera not shared between the two regions rather than differences within genera shared between the two regions.

When considering the relative contributions of shared versus unique genera to regional functional richness, we found that in eastern North America, 18.5% of the total functional richness was uniquely contributed by species from genera unique to that data set, and 81.5% was contributed by genera shared between the two data sets. In Europe, 9.1% of the functional richness was uniquely contributed by species from genera unique to the European data set, and 90.9% was contributed by species from shared genera (fig. 4). Using the percent contributions from the species richness analyses, we performed a $\chi^2$ goodness-of-fit test for each data set. This analysis was designed to ask whether the observed functional-richness contributions from unique and shared genera are any different from that expected given their species richness contributions. In Europe, we found that the observed functional-richness contributions did not deviate from that expected given the observed species richness contributions ($\chi^2 = 0.4054$, df $= 1$, $P = .5243$). In other words, shared and unique genera contribute proportionally to both species richness and functional richness in Europe. Conversely, in eastern North America, the species from genera unique to that data set have a significantly lower contribution to the observed functional richness than expected given their percent contribution to the observed species richness ($\chi^2 = 33.499$, df $= 1$; $P < .001$). In other words, species from genera unique to the eastern North American data set that drive the species richness anomaly generally add species within the functional volume already occupied by species from genera shared with Europe, and they add very little to the periphery of the functional space.

## Discussion

Biodiversity gradients are among some of the most scrutinized patterns in biology, broadly, and in ecology and evolution in particular (Hillebrand 2004; Mittelbach et al. 2007). Species richness anomalies, where species richness in one region is much higher than that in another climatically similar region, are powerful natural experiments that have been influential in our understanding of the relative importance of regional-scale processes and the general importance of differential biogeographic histories (Ricklefs 2004; Kissling et al. 2012*a*, 2012*b*). Here, we have investigated the relationship between species richness and functional richness in the context of the eastern North American–European tree species-diversity anomaly. A key goal was to investigate the classic

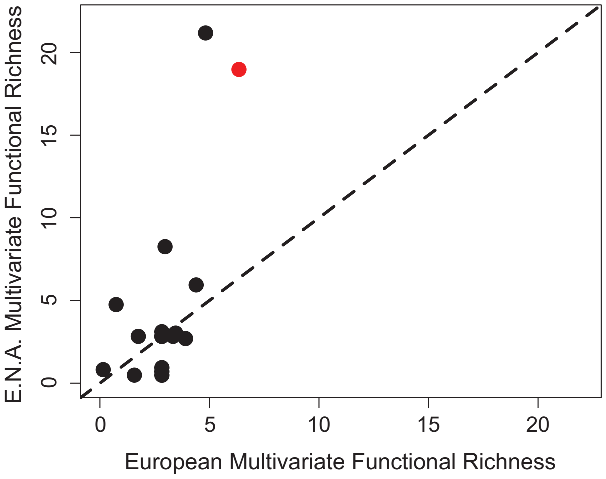

**Figure 3:** A total of 16 genera with two or more species were shared between the eastern North American and European tree data sets. The functional richness within each of these genera in the eastern North American (E.N.A.) data set is plotted against the species richness for those genera in the European data set (black circles). The genus with the largest deviation was *Quercus*. A paired *t*-test found no difference between the functional richness within genera between the two data sets ($t = -1.0815$, df $= 15$, $P = .2965$). The red circle indicates the total functional richness for species from genera unique to the eastern North American data set plotted against the total functional richness for species from genera unique to the European data set. The dashed line is the 1 : 1 line.

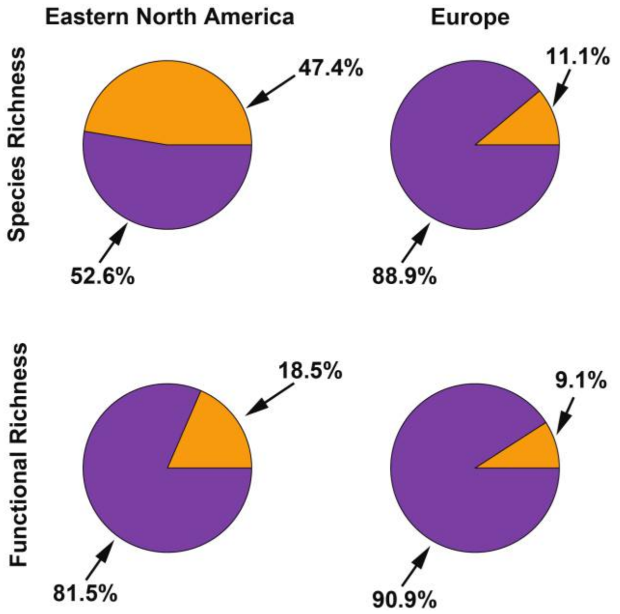

**Figure 4:** Percent of the species richness and functional richness contributed by species from genera shared between the two data sets (purple) and by species from genera unique to each data set (orange). Results from a $\chi^2$ goodness-of-fit test show that the percent of the functional richness in Europe contributed by unique and shared genera is no different from that expected given their percent contributions to the species richness ($\chi^2 = 0.4054$, df $= 1$, $P = .5243$). Conversely, the percent of the functional richness contributed by species from unique genera in eastern North America is significantly less than expected given their percent contribution to the species richness ($\chi^2 = 33.499$, df $= 1$, $P < .001$).

question of whether species richness increases via niche partitioning and limiting similarity, thereby resulting in an expansion of the total functional space occupied by co-occurring species, or whether regional-scale climatic constraints on phenotypic space keep levels of functional richness constant across a species richness anomaly.

Our results show that the functional richness, quantified as the multivariate functional convex hull volume (functional richness), is asymptotically related to species richness on both continents and across spatial scales (figs. 1, A1, A2). While our analyses cannot definitively state that functional richness hits a limit or ceiling as species richness increases, the results do support a continuous deceleration in function-richness increase with increasing species richness. Further, when comparing fits from nonlinear asymptotic Michaelis-Menten models with linear models, we found that the nonlinear models had lower AIC values (table A1). We also quantified the degree of species packing into multivariate functional space as species diversity increases, with the expectation that niche differentiation and limiting similarity would maintain a constant degree of packing. In contrast, we found that the degree of packing in trait space increased with species diversity in both regions (figs. 1, A1, A2). Taken together, both of these results reject a limiting-similarity or niche-partitioning hypothesis to explain differences in species richness levels in the two regions. Rather, our results indicate that the similar climates between the two regions place a constraint on the total functional space that can be occupied, and differential net diversification within that constrained opportunity space underlies the richness anomaly (Ricklefs and Latham 1999; Ricklefs et al. 2004). One important caveat worth consideration is that our data sets lack information regarding intraspecific trait distributions and interspecific overlaps in those distributions. Thus, we cannot definitively say that species are not simply more finely partitioning a climatically constrained trait space in species-rich assemblages.

To further investigate whether map grid cells on different continents were functionally similar due to similar climates, we performed a series of Mantel tests where the mean nearest trait neighbor was related to the climatic dissimilarity. Across scales and continents, we found that these two dissimilarities were positively correlated, indicating that functionally similar assemblages in map grid cells on different continents tended to occupy similar climates.

The asymptotic relationship between functional richness and species richness contrasts with a result reported by Swenson and Weiser (2014) for eastern North American tree assemblages. The disparity in our results and those of Swenson and Weiser (2014) can be explained by three main differences between the studies. First, Swenson and Weiser (2014) examined small-scale forest inventory plots, while our study analyzed large-scale assemblages derived from range maps, indicating that functional space may not saturate until larger regional scales. Second, both works analyzed maximum height, seed mass, and wood density, but our study analyzed leaf size, and the previous study used leaf nitrogen. Third, our study analyzed trees defined as freestanding woody plants >10 m tall, whereas the previous study included many smaller-statured species inventoried >2.54 cm. These differences highlight that the addition of more traits or life-forms may lead to a more linear relationship between functional space and species richness. Thus, because it is not currently feasible to perform comparative research across the tree anomaly with more traits and life-forms and because tree phenotypes are certainly more complex than that typically measured in trait-based tree ecology (Swenson 2013), we caution that future research that can include more traits and/or life-forms may find a more linear relationship or, more likely, saturation not being reached until higher levels of species richness are sampled. Further, it is also important to note that limiting similarity may not be as easily detected using range map data instead of inventory plot data.

We next compared the species richness and functional richness within genera that were shared between the study regions or were unique to a single study region. We found that the species richness and functional richness within shared genera were not significantly different between the two study regions (figs. 2, 3). Specifically, the species richness or functional richness of a genus in eastern North America was no higher, on average, than the species richness or functional richness of that same genus in Europe. An exception to this general pattern was the oak genus, *Quercus*, which had far higher species richness and functional richness in eastern North America, but it was not enough to cause an overall significant result. The deviating results for *Quercus* may reflect that this very large genus contains multiple old, well-defined clades (subgenera or sections), several of which are endemic to either North America or Eurasia (Manos et al. 1999). Notably, the American endemic section *Lobatae* (black oaks) contributes much of the species richness and functional richness of oaks in eastern North America.

When considering those genera only unique to one region or another, we found that the species richness and functional richness of genera unique to eastern North America was far higher than that of the genera unique to Europe. The disproportional contribution to the species richness anomaly of species from genera unique to eastern North America versus species from genera unique to Europe suggests that the diversity is largely explained by historical processes, either a lack of dispersal or differential extinction. The well-studied paleobotanical record from the two records shows that the difference primarily reflects extinctions, as most currently uniquely American genera occurred in Europe during the Neogene (e.g., *Carya*, *Chamaecyparis*, *Gymnocladus*, *Liriodendron*, *Magnolia*, *Robinia*, *Taxodium*, and *Tsuga*). Many of these also occur in East Asia, where extinctions were also relatively less common (Latham and Ricklefs 1993*a*). These historical processes could be related to the functional space those unique genera occupy. For example, a genus unique to eastern North America that contributes disproportionately to the regional-scale species richness may do so because it occupies a unique niche or functional space where it has diversified, and we would expect a concomitant disproportional contribution of that genus to the regional-scale functional richness. We tested this hypothesis by quantifying the species richness in each region contributed by species from genera unique to one region or the other and by species from shared genera. In eastern North America, we found that 47.4% of the species richness is attributable to species from genera not found in Europe, whereas 11.1% of the species diversity in Europe is attributable to species from genera not found in eastern North America (fig. 4). We used these percentages to set an expected level of continental-scale functional richness contributed by each group. We found that genera unique to eastern North America contribute only 18.5% to the overall continental functional richness. Indeed, these unique genera contribute disproportionately and significantly less to the overall functional richness than would be expected given their level of species diversity (fig. 4). The genera unique to Europe contribute 9.1% to the overall functional richness, which was no greater or less than that expected given their contribution to the continental species diversity. Thus, although species from genera unique to eastern North America contribute disproportionately to the species richness anomaly and provide nearly 20% of the eastern North American functional richness, the latter contribution is less than expected from their richness. We therefore reject the hypothesis that these genera simply diversified into novel functional space, thereby permitting a greater overall number of species in eastern North America. Rather, they have nevertheless diversified and persisted in their own constrained regions of functional space.

The results shown here demonstrate that the functional richness of species assemblages is asymptotically related to species richness on both continents at multiple spatial scales, thereby suggesting a smaller role for limiting similarity in driving the species richness anomaly and a much larger role for differential net diversification rates (figs. 1, A1, A2). The results also show that the eastern North American–European tree species richness anomaly is largely driven by species from genera unique to the former. However, the species from these genera occupy less novel functional space than expected and therefore overlap substantially in functional space with the genera shared between the two regions (figs. 2–4). Taken together, the results indicate that despite the species richness anomaly between the two continents, continental-scale functional richness or overall niche volume is likely similarly constrained due to their similar climatic conditions, and that a greater exploration of the functional space in one region does not explain the species richness anomaly. This conclusion is buoyed by the finding that genera unique to eastern North America driving the species richness anomaly do not do so by being extraordinarily functionally unique. Rather, they overlap substantially in functional space with the species from genera that are shared between continents. In sum, the results point to a strong role for historical biogeography (e.g., allopatry increasing speciation rates, continuous land mass during glaciation reducing extinction rates) and a weaker role for limiting similarity in generating the species richness anomalies.

## Acknowledgments

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# APPENDIX A

## Comparisons of Linear and Nonlinear Regression Models and Graphs of 25 × 25-km and 250 × 250-km Analyses

**Table A1:** Akaike information criterion (AIC) values for a standard ordinary least squares linear model and a nonlinear asymptotic Michaelis-Menten model with multivariate functional richness regressed onto species richness

| Region and spatial scale of map grid cell (km) | Linear model AIC | Nonlinear Michaelis-Menten model AIC |
|---|---|---|
| Eastern North America: | | |
| 25 × 25 | 95706.48 | 88457.24 |
| 50 × 50 | 20201.27 | 19545.57 |
| 250 × 250 | 1396.06 | 1243.31 |
| Europe: | | |
| 25 × 25 | 29340.7 | 27687.23 |
| 50 × 50 | 7373.87 | 6970.97 |
| 250 × 250 | 286.36 | 268.96 |

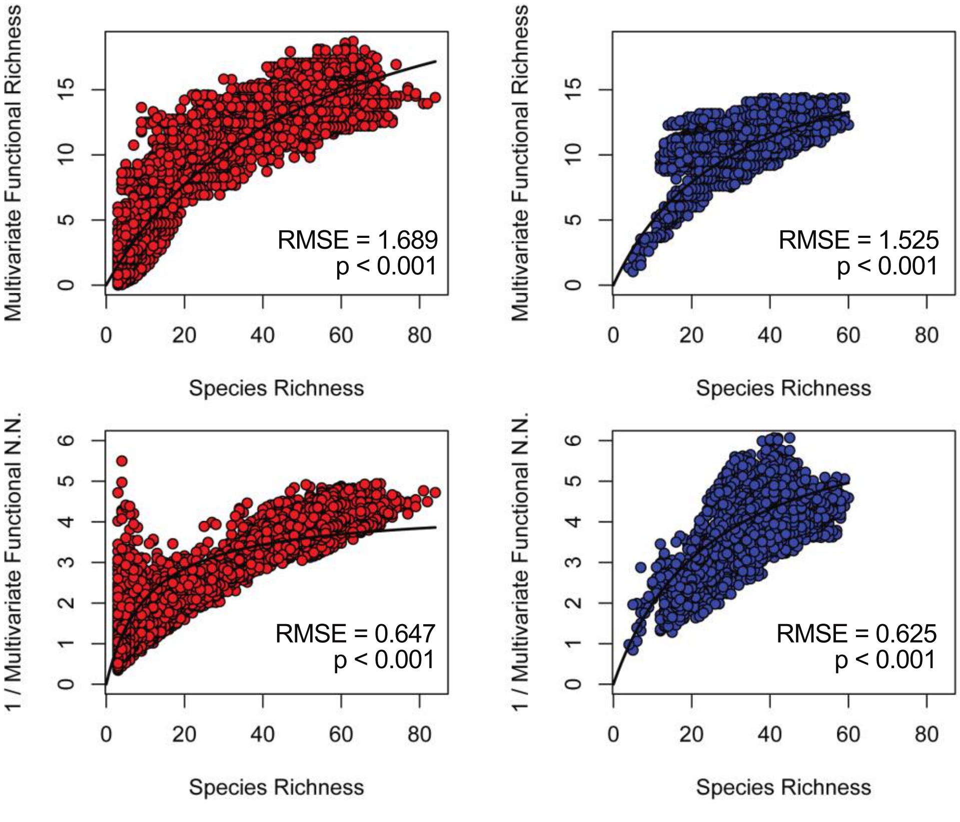

**Figure A1:** Relationship between volume and packing of trait space and tree species richness in 25 × 25-km map grid cells in eastern North America and Europe, fit with a Michaelis-Menten model. The top row plots the multivariate functional richness (i.e., the multivariate trait volume) against the species richness. The bottom row plots the inverse of the mean nearest neighbor (N.N.) distance in multivariate trait space between species in a map grid cell. The *P* value is from the significance test of the asymptotic parameter in the Michaelis-Menten model. RMSE = root mean square error.

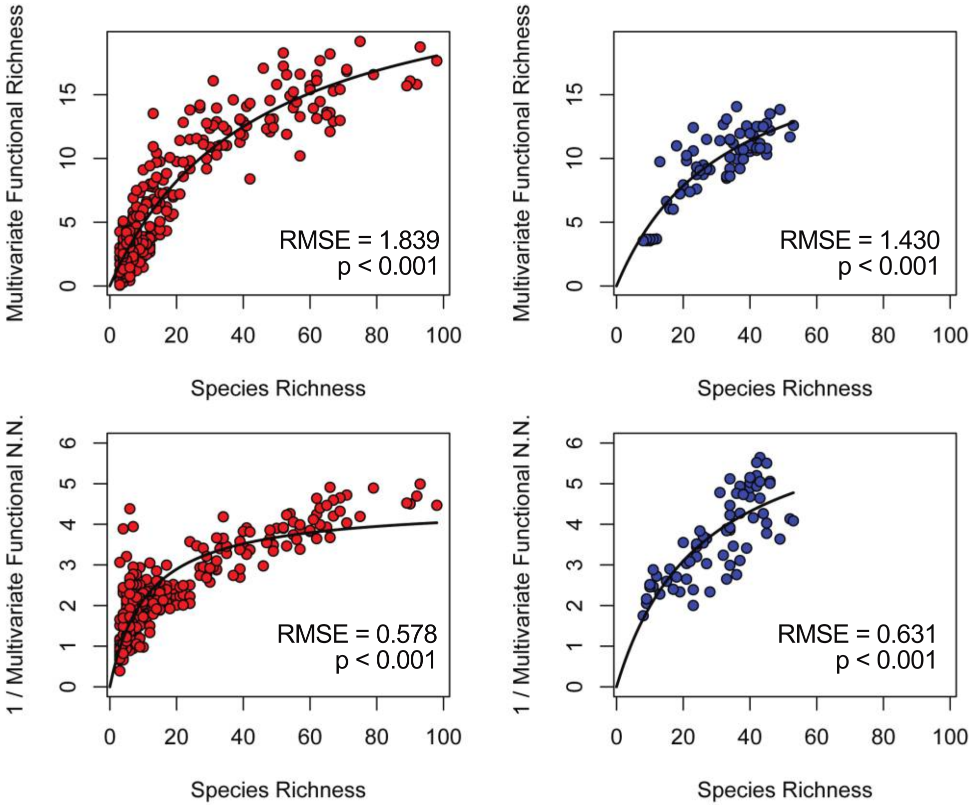

**Figure A2:** Relationship between volume and packing of trait space and tree species richness in 250 × 250-km map grid cells in eastern North America and Europe, fit with a Michaelis-Menten model. The top row plots the multivariate functional richness (i.e., the multivariate trait volume) against the species richness. The bottom row plots the inverse of the mean nearest neighbor (N.N.) distance in multivariate trait space between species in a map grid cell. The *P* value is from the significance test of the asymptotic parameter in the Michaelis-Menten model. RMSE = root mean square error.

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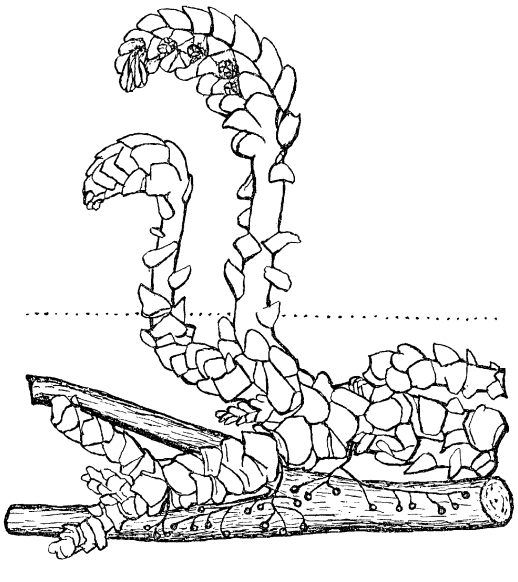

"*Lathræa squamaria*; pen-sketch after Kerner. The dotted line represents the surface of the soil. Only a small part of the underground stems and branches is shown in the figure, together with tendrils bearing the pediculate haustoria." From "The Phenogamous Parasites" by Charles A. White, *The American Naturalist* (1908, 42:12–33).