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# Functional beta-diversity patterns reveal deterministic community assembly processes in eastern North American trees

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## ABSTRACT

**Aim** Determining the relative influence of niche-based and neutral processes in driving the spatial turnover of community composition is a central challenge in community ecology. Spatial patterns of functional turnover, or functional beta diversity, may capture important signals of niche-based assembly processes, but these patterns have not been quantified for communities across broad geographic and environmental gradients. Here, we analyse continental-scale patterns of species and functional beta diversity in relation to space and the environment to assess the relative importance of niche-based and neutral community assembly mechanisms.

**Location** Eastern North America.

**Methods** We use a continental-scale forest plot dataset and functional trait data to quantify spatial patterns of species and functional beta diversity. We use redundancy analysis-based variance partitioning to evaluate the influence of space, soil and climate on beta-diversity metrics. We use a null model approach to test for non-random functional beta diversity given the observed patterns of species turnover across spatial scales.

**Results** Species and functional beta diversity increased with increasing geographic distance (i.e. distance decay of community similarity). Results of variance partitioning analysis show that species and functional beta diversity were spatially structured and significantly related to environmental, particularly climatic, variation. Results of null model analysis show that functional beta diversity was lower than expected based on species turnover at fine scales (< 600 km) and higher than expected at broad scales (> 1800 km).

**Main conclusions** The observed patterns of functional beta diversity support a niche-based model of community assembly, driven by the deterministic filtering of species across environmental gradients based on their functional traits.

## Keywords

**Beta diversity, community assembly, eastern North America, environmental filtering, functional traits, species turnover, temperate forest, trees.**

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## INTRODUCTION

A major goal in ecology is to determine the mechanisms underlying the structure and assembly of communities. Quantifying patterns of species turnover or species beta diversity in space has been one of the key tools in this effort (Whittaker, 1960; Legendre

*et al.*, 2005). In particular, patterns of distance decay, the decrease in similarity of community composition (or increase in species beta diversity) with increasing geographic distance, have been used to infer various community assembly mechanisms (Nekola & White, 1999; Condit *et al.*, 2002; Tuomisto *et al.*, 2003). A limitation of this approach is that niche-based and

neutral assembly processes are expected to produce similar distance decay patterns (Soininen *et al.*, 2007). Under niche-based assembly, species are deterministically filtered by the local environment based on their functional attributes (Keddy, 1992; Weiher *et al.*, 1998). Niche-based distance decay occurs due to the decrease in environmental similarity with increasing geographic distance (Nekola & White, 1999; Gilbert & Lechowicz, 2004). Distance decay can also result from neutral processes such as dispersal limitation, speciation and ecological drift (Hubbell, 2001). Measures of species beta-diversity are therefore of potentially limited use for determining the relative roles of niche-based versus neutral assembly processes.

A key weakness of species beta diversity metrics is that they ignore functional similarities between communities. Niche-based community assembly involves the deterministic filtering of species based on their functional traits. Patterns of functional turnover between communities (i.e. functional beta diversity) may therefore capture important signals of niche-based assembly processes that are not evident from patterns of species beta diversity (Swenson *et al.*, 2011). For example, consider a case in which two communities inhabit similar environments. If environmental filtering is driving community assembly, this could be detected by the high functional similarity (low functional beta diversity) of the two communities (Matsui *et al.*, 2002; Smith & Wilson, 2002). However, communities with similar functional composition may still have high species turnover (Chase, 2003; Fukami *et al.*, 2005). Measuring only species beta diversity between the communities would therefore reveal little about community assembly processes. Disparities between levels of species and functional beta diversity are also evident at broad, biogeographic scales. For example, the temperate floras of Europe, Asia and the Americas share few species (high species beta diversity) but are similar in their phylogenetic and functional composition (Qian & Ricklefs, 2000). High rates of dispersal limitation and large numbers of functionally equivalent species may cause disparities between species and functional turnover at both regional and local scales.

Given the limited ability of species beta-diversity metrics to detect the processes underlying community assembly, it is not surprising that the functional beta diversity of communities is increasingly measured (Ricotta & Burrascano, 2008; Swenson *et al.*, 2011, 2012). Several of the more compelling cases for measuring functional beta diversity have come from analysing the functional versus species dissimilarities of communities through time. In the first example, Fukami *et al.* (2005) quantified the temporal turnover of experimental plant assemblages in the Netherlands. This work showed that functional composition converged over time whereas there was no convergence in species composition. Helsen *et al.* (2012) observed similar patterns in a chronosequence of restored semi-natural grassland communities. These studies demonstrated the importance of niche-based processes in driving community turnover and the necessity of analysing functional composition to detect these patterns. Similarly, recent work by Swenson *et al.* (2012) has shown that while the species composition of tropical tree communities may appear to be neutrally drifting through time,

the temporal turnover in the functional composition is highly deterministic. Thus in these cases, faulty inferences regarding the importance of neutral dynamics would have been produced if the turnover of the functional composition were never quantified.

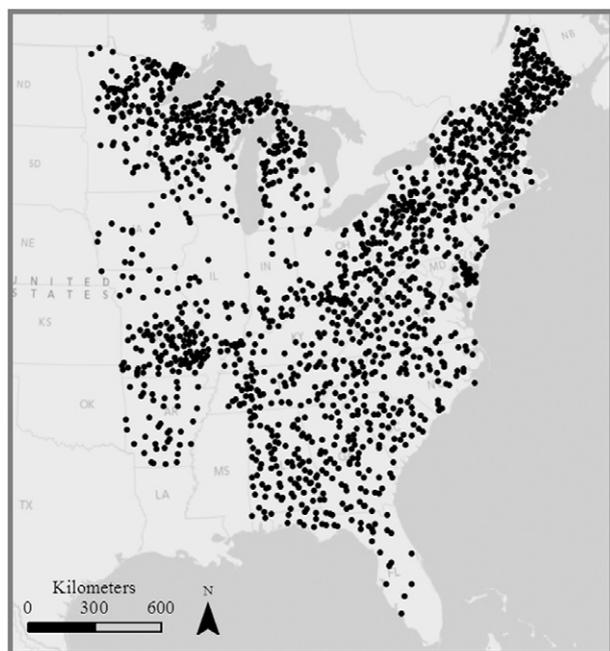
Although recent work has begun to examine functional beta diversity through time and across local environmental gradients (Swenson *et al.*, 2011, 2012), spatial patterns of functional beta diversity across broad, continental-scale gradients have not been investigated. In addition, little is known about how spatial patterns of functional beta diversity are influenced by the spatial structure of key environmental filters. Filtering by environmental factors with fine-scale spatial distributions (e.g. many edaphic variables) is expected to produce different patterns of distance decay than filtering by factors with broad-scale gradients (e.g. climatic variables; Palmer, 2007; Siefert, 2012). Understanding the spatial relationships between environmental filters and functional beta diversity may offer powerful insights into the processes that drive community assembly from local to continental scales.

In this study, we analysed patterns of species and functional beta diversity to assess the relative importance of niche-based and neutral assembly mechanisms in eastern North American tree communities. We combined a continental-scale forest plot dataset with species functional trait data to quantify species and functional beta diversity across broad geographic and environmental gradients. Specifically, our objectives were to: (1) describe and compare spatial patterns of species and functional beta diversity; (2) determine the degree to which species and functional beta diversity are explained by space, soil and climate; and (3) assess whether functional beta diversity is greater than or less than expected based on observed levels of species beta diversity across multiple spatial scales, using a null model approach (Swenson *et al.*, 2011). Random levels of functional beta diversity given the observed amount of species turnover indicate neutral assembly processes, whereas higher or lower than expected functional beta diversity provides evidence of deterministic, niche-based assembly processes. We hypothesized that functional beta diversity would be lower than expected at small geographic distances due to functional convergence in similar environments and higher than expected at large geographic distances due to directional shifts in functional composition across broad-scale environmental gradients.

## METHODS

### Species composition data

We obtained data on species composition from the United States Department of Agriculture Forest Inventory and Analysis program (FIA). FIA plots are georeferenced, although coordinates are 'fuzzed' by as much as 0.8 km from the original plot location, a scale which is inconsequential for this analysis. FIA plots consist of four circular 0.017-ha subplots where all stems > 12.7 cm in diameter are inventoried. Within each subplot is a 0.001-ha microplot where all stems > 2.54 cm in diameter are



**Figure 1** Map of the study area (Albers projection). Points show locations of forest plots included in the dataset.

inventoried. Stems from all subplots and microplots within a given plot were pooled in this analysis. Inventories were taken from 2001–06. When multiple inventory years were available for a given plot, we took data from the most recent inventory. The study area encompassed the states located east of 98° E (no data were available for Louisiana or Mississippi; Fig. 1). We restricted the dataset to plots that contained at least 20 total stems and had associated soil data. The final dataset included 1598 plots in 28 states containing 60,813 individual trees representing 173 species.

### Environmental data

We obtained soil data from the FIA database, using data from soil samples collected from the upper mineral layer (0–4 cm depth) in one subplot per plot. Eight edaphic variables were included in the analysis: total water content (%), coarse fraction (percentage of mineral soil greater than 2 mm in size), organic carbon (%), total nitrogen (%), pH, exchangeable K ( $\text{mg kg}^{-1}$ ), exchangeable Mn ( $\text{mg kg}^{-1}$ ) and effective cation exchange capacity ( $\text{cmol}_c \text{kg}^{-1}$ ).

We extracted climate data for each plot from the WorldClim database, a global climate database with a spatial resolution of 1  $\text{km}^2$  (Hijmans *et al.*, 2005). Six variables were included in the analysis: maximum temperature, minimum temperature, temperature seasonality (standard deviation of monthly mean temperature), precipitation in the driest month, precipitation in the wettest month and precipitation seasonality (coefficient of variation of monthly precipitation).

### Functional trait data

We included four functional traits in the analysis: maximum height, seed mass, leaf nitrogen content and wood density. These traits were selected because they relate to important aspects of plant strategy and represent multiple independent axes of functional variation (Swenson & Weiser, 2010). Maximum height is an indicator of the adult light niche and represents the tradeoff between light acquisition and stem construction costs (Westoby *et al.*, 2002; Moles *et al.*, 2009). Seed mass is an indicator of regenerative strategy and represents the tradeoff between seed output and seed size (Venable, 1992; Moles & Westoby, 2006). Leaf nitrogen content indicates a plant's position on the leaf economics spectrum, which describes the tradeoff between rapid resource uptake and growth versus resource conservation and leaf life span (Wright *et al.*, 2004; Shipley *et al.*, 2006). Wood density indicates a plant's position on the wood economics spectrum (Chave *et al.*, 2009), which describes the tradeoff between rapid growth and mechanical support. Previous studies have demonstrated that these traits are subject to abiotic and biotic filtering and vary across environmental gradients (e.g. Murray *et al.*, 2004; Wright *et al.*, 2004; Swenson & Enquist, 2007; Cornwell & Ackerly, 2009; Swenson & Weiser, 2010), making them potentially useful indicators of deterministic community assembly processes. They have also been widely measured and reported for tree species in the eastern United States. We obtained trait values for all species in the dataset from the literature and publicly accessible online trait databases as described in Swenson & Weiser (2010). When more than one value was available for a given species, a mean value was calculated, and each individual in the dataset was assigned the mean trait value of its species. Our analysis therefore does not account for intraspecific trait variation. For each plot, we calculated the abundance-weighted mean trait value for each trait using the species mean values. Plot mean seed mass and maximum height values were log transformed to improve normality.

### Data analysis

We examined spatial patterns of environmental variation and species and functional beta diversity using distance decay plots, which describe the decrease in similarity between two observations as the geographic distance between them increases (Nekola & White, 1999). A decrease in similarity with increasing distance indicates that a variable is spatially structured (i.e. spatially dependent or autocorrelated).

Geographic distance was calculated as great-circle distance, the shortest line between plot locations taking the curvature of the earth into account. Edaphic and climatic dissimilarity were calculated as Euclidean distance using plot edaphic and climatic characteristics. Due to collinearity among edaphic and climatic variables, we ran principal components analyses (PCA) on edaphic and climatic data and used plot PCA axis scores rather than raw data to calculate dissimilarities. For soil, we used the first four PCA axes, which accounted for 89% of the total edaphic variation. For climate, we used the first two PCA axes,

which accounted for 89% of the total climatic variation. Dissimilarity in species composition (species beta diversity) was calculated as Bray–Curtis distance using species abundance data. Values range from 0, indicating identical species composition and abundance, to 1, indicating complete species turnover. Functional dissimilarity (functional beta diversity) was calculated as Euclidean distance using plot mean trait values. Values of each trait were standardized to  $Z$ -scores (mean = 0, SD = 1) to control for differences in variance and units of measurement among traits. Multivariate functional dissimilarity was calculated using all four traits together, and univariate functional dissimilarity was calculated using each trait individually. Functional dissimilarity values are unitless and unbounded, with larger values indicating greater distance between plots in trait space.

The dissimilarity metrics described above were calculated for each pair of plots in the dataset. Due to the large number of plot pairs (*c.* 1.3 million), we binned plots pairs by geographic distance (50,000 pairs per bin) and calculated the mean dissimilarity of each bin to improve clarity of the distance decay plots. Because raw values of the different dissimilarity metrics are not directly comparable, we compared the strength of distance decay (*i.e.* spatial structure) among metrics using a spatial structure index (SSI), calculated as the percentage increase in dissimilarity from the smallest to the largest distance bin. A greater SSI value indicates a greater increase in dissimilarity with increasing geographic distance, relative to the amount of dissimilarity at the smallest distance (*i.e.* stronger distance decay).

We determined the degree to which species and functional beta diversity were explained by spatial, edaphic and climatic factors using variance partitioning based on redundancy analysis (RDA; Borcard *et al.*, 1992). We used principal coordinates of neighbour matrices (PCNM) to generate spatial explanatory variables capturing the spatial relationships among plots at all scales (Borcard & Legendre, 2002). Due to the large number of spatial and environmental variables, we used forward selection (Blanchet *et al.*, 2008) to generate more parsimonious sets of spatial, edaphic and climatic explanatory variables. We ran separate forward selection and variance partitioning for species beta diversity, functional beta diversity and individual functional traits. Variance partitioning analysis partitioned the variation in each response matrix or variable into eight components: (a) pure spatial, (b) pure edaphic, (c) pure climatic, (d) shared spatial-edaphic, (e) shared edaphic-climatic, (f) shared spatial-climatic, (g) shared spatial-edaphic-climatic, and (h) unexplained variation. The amount of variance explained by each component was estimated using adjusted  $R^2$  values (Peres-Neto *et al.*, 2006) and the significance of components was tested by permutation tests (Borcard *et al.*, 1992). Species abundance data were Hellinger transformed (Legendre & Gallagher, 2001) prior to analysis. The PCNM analysis, variance partitioning and tests of significance of components were conducted using the ‘vegan’ package (Oksanen *et al.*, 2012) and forward selection was conducted using the ‘packfor’ package (Dray *et al.*, 2011) in R (R Core Team, 2012).

## Null model analysis

A major goal of this study was to determine whether functional beta diversity at a given scale was greater than or less than expected given the observed level of species beta diversity. We tested this using a null model approach. During each iteration of the null model, trait values were randomized among species in the dataset and pairwise functional dissimilarities between all plots were calculated. This null model generates expectations of functional beta diversity under the assumption that species turnover is random with respect to functional traits, while maintaining the observed levels of species richness and relative abundances, species spatial distributions and species beta-diversity patterns (Swenson *et al.*, 2011). We used 1000 iterations of the null model to obtain null distributions of multivariate and single-trait functional dissimilarity for each geographic distance bin. We evaluated departures of observed functional dissimilarity from the null expectations by calculating standardized effect sizes (SES; Gotelli & Graves, 1996):

$$SES = (X_{\text{obs}} - X_{\text{null}}) / SD(X_{\text{null}}),$$

where  $X_{\text{obs}}$  is the observed dissimilarity,  $X_{\text{null}}$  is the mean of the null distribution and  $SD(X_{\text{null}})$  is the standard deviation of the null distribution. SES values greater or less than 1.96 indicate that the observed functional beta diversity is significantly higher or lower than expected, respectively. Departures from the null expectations indicate that species turnover between plots separated by a given distance is non-random with respect to functional traits, providing evidence of deterministic community assembly processes.

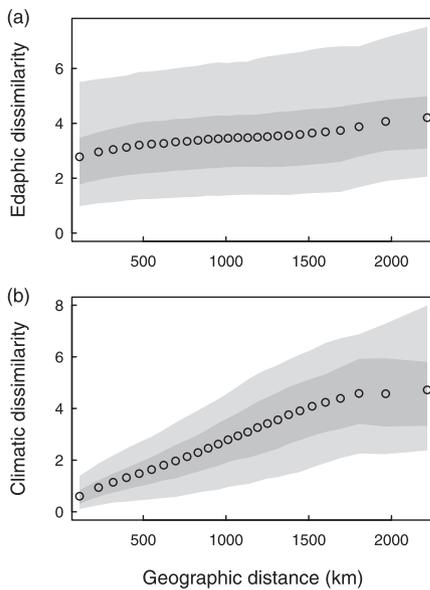
The null model was also used to evaluate whether the overall rate of distance decay of functional similarity, measured as the slope of the relationship between functional dissimilarity and geographic distance, was different than expected given the observed species turnover. Positive SES values for slope indicate faster than expected distance decay of functional similarity, and negative values indicate slower than expected distance decay.

## RESULTS

### Spatial patterns

Edaphic and climatic dissimilarity increased continuously with increasing geographic distance (Fig. 2), indicating that environmental variation was spatially structured across all scales. Edaphic variation had relatively weak spatial structure, with high dissimilarity at small distances and only a slight increase with increasing distance (SSI = 51%; Fig. 2a), whereas climatic variation had much stronger spatial structure (SSI = 679%; Fig. 2b).

Species and functional beta diversity (*i.e.* dissimilarity in species composition and functional traits) increased continuously with increasing geographic distance (Fig. 3a, b). Species beta diversity tended to be high even at the smallest distances and increased only moderately with increasing distance, reflect-



**Figure 2** Distance decay plots showing the increase in environmental dissimilarity with increasing geographic distance between forest plots in the eastern United States. Pairwise dissimilarities were calculated for each pair of plots in the dataset and binned by geographic distance (50,000 pairs per bin). Points represent the mean dissimilarity, dark grey areas represent the central 50% of the distribution and light grey areas represent the central 95% of the distribution for each distance bin. Spatial structure index (percentage increase in dissimilarity from first to last distance bin): edaphic: 51%, climatic: 679%.

ing weak spatial structure (SSI = 28%; Fig. 3a). In comparison, functional beta diversity was relatively low at small distances and was more strongly spatially structured (SSI = 77%; Fig. 3b). Dissimilarity of individual functional traits also increased with geographic distance (Fig. 3c–f), with seed mass and wood density displaying stronger spatial structure than maximum height or leaf nitrogen content (Fig. 3c–f).

### Variance partitioning

Of the 844 spatial explanatory variables generated by PCNM, forward selection retained 85 for modelling species beta diversity and 128 for functional beta diversity. Forward selection retained all edaphic and climatic variables for modelling species beta diversity and all but one (soil coarse fraction) for modelling functional beta diversity (see Appendix S1 in Supporting Information). For both species and functional beta diversity, the first three edaphic variables selected were pH, effective cation exchange capacity and exchangeable K; the first three climatic variables selected were maximum temperature, precipitation seasonality and temperature seasonality (see Appendix S1).

Results of the variance partitioning analysis show that species and functional beta diversity were significantly related to space, soil and climate (Fig. 4a, b). Of the three sets of explanatory variables, space explained the most variation in both species

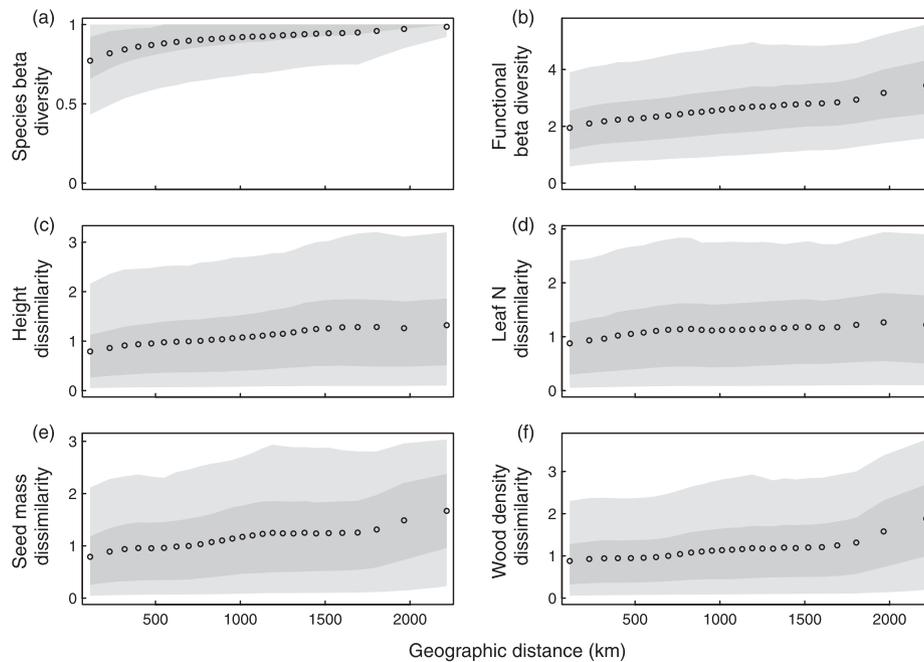
composition (27%; Fig. 4a) and functional traits (44%; Fig. 4b), followed by climate (13 and 21%; Fig. 4a, b), then soil (8 and 15%; Fig. 4a, b). Most of the environmentally explained variation was spatially structured (i.e. shared spatial–edaphic, spatial–climatic and spatial–edaphic–climatic components; Fig. 4a, b). Spatial structure unassociated with the environment (i.e. the pure spatial component) explained 12% of the variation in species composition (Fig. 4a) and 18% of the variation in functional traits (Fig. 4b). Variance partitioning for individual functional traits showed similar patterns (Fig. 4c–f), with the exception that variation in leaf nitrogen content was better explained by soil than by climate (Fig. 4c).

### Null model analysis

Using the null model that preserved the observed species beta diversity while randomizing functional traits, functional beta diversity was expected to increase with increasing geographic distance. However, the observed increase in functional beta diversity with distance was more rapid than the null expectation (Fig. 5a), indicating that species turnover was non-random with respect to functional traits. Functional beta diversity at small distances (< 600 km) was significantly less than the null expectation, indicating that nearby plots were more functionally similar than expected based on random species turnover. Conversely, functional beta diversity at large distances (> 1900 km) was significantly greater than the null expectation, indicating that spatially distant plots were more functionally dissimilar than expected. Null model analysis of individual traits produced similar results (Fig. 5b–e). Trait dissimilarity was generally lower than expected at small distances and higher than expected at large distances, with the exception of leaf nitrogen content, which did not differ significantly from the null expectation at any distance (Fig. 5c).

### DISCUSSION

The present study used a continental-scale forest plot dataset and species functional trait data to assess the relative importance of niche-based and neutral processes in driving species and functional beta diversity of tree communities in eastern North America. The results show that similarities in species and functional composition of tree communities decayed with increasing geographic distance (Fig. 3). Species and functional beta diversity were significantly related to climatic and (to a lesser extent) edaphic factors, providing evidence of deterministic environmental filtering. Because the environment, particularly climate, was strongly spatially structured at the scales examined in our study (Fig. 2), this environmental filtering contributed to the observed distance decay of community similarity. Our analysis detected additional spatial structure in the species and functional composition data that was not related to the environment (i.e. a pure spatial component; Fig. 4). The pure spatial component in variance partitioning analyses is often interpreted as evidence of neutral processes, i.e. dispersal limitation (Gilbert & Lechowicz, 2004; Cottenie, 2005), but it could also reflect filter-



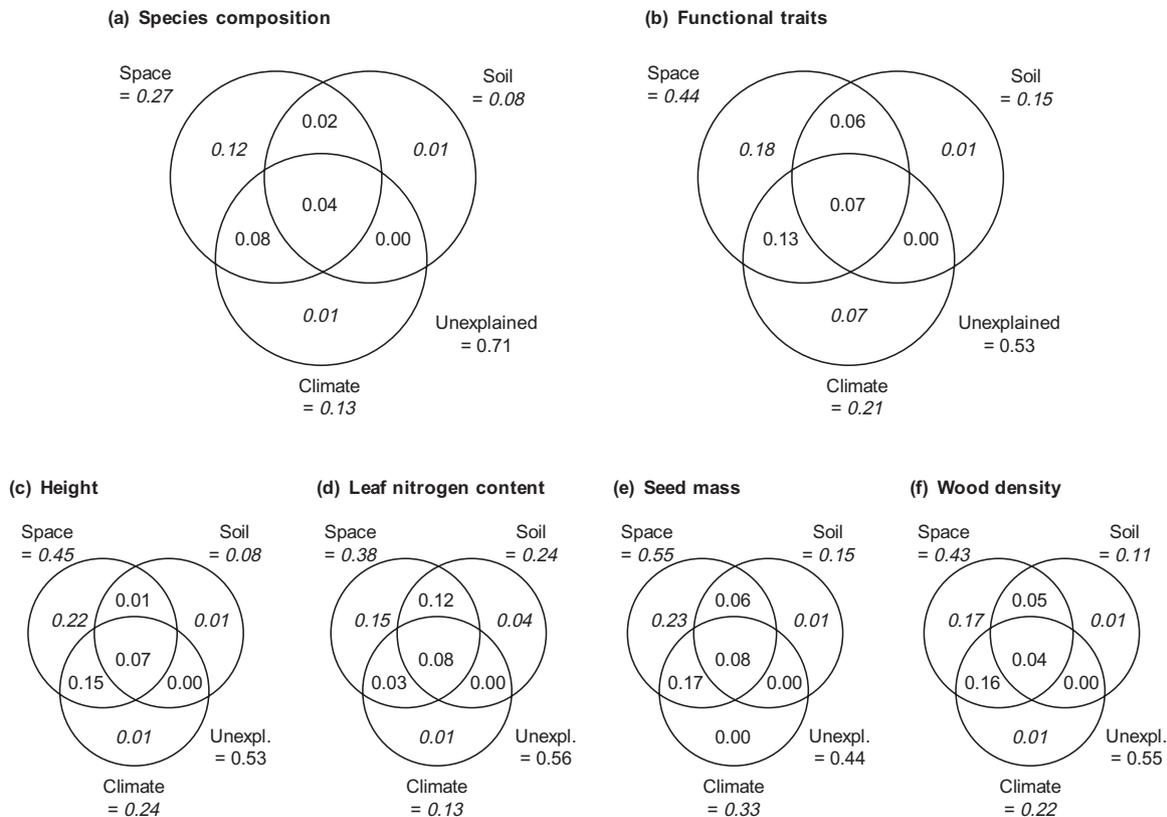
**Figure 3** Distance decay plots showing the increase in beta-diversity metrics with increasing geographic distance between forest plots in the eastern United States. Pairwise dissimilarities were calculated for each pair of plots in the dataset and binned by geographic distance (50,000 pairs per bin). Points represent the mean dissimilarity, dark grey areas represent the central 50% of the distribution and light grey areas represent the central 95% of the distribution for each distance bin. Spatial structure index (percentage increase in dissimilarity from first to last distance bin): species beta diversity 28%, functional beta diversity 77%, height 67%, leaf nitrogen content 67%, seed mass 111%, wood density 114%.

ing by unmeasured, spatially structured environmental variables (Legendre *et al.*, 2005). While we conclude that deterministic environmental filtering plays a key role in driving species and functional beta diversity, we cannot rule out the potential influence of dispersal limitation.

We were interested in whether species and functional beta diversity differed in the degree to which they were influenced by spatial, edaphic and climatic factors. Although the explanatory variables explained more variation in functional traits than in species composition in general, the relative contributions of space, soil and climate were similar for species and functional beta diversity (Fig. 4). In addition, the subsets of edaphic and climatic variables chosen by forward selection to model species composition and functional traits were nearly identical (see Appendix S1). This is perhaps not surprising, given that species and functional beta diversity were correlated (Mantel's  $r = 0.46$ ;  $P < 0.001$ ). While climatic factors were more important than edaphic factors in driving overall functional turnover at the broad spatial scales examined in this study (Pakeman *et al.*, 2009), the relative influence of edaphic and climatic factors varied among the four individual traits, indicating that traits differ in the strength of their responses to specific environmental filters. For example, leaf nitrogen content was the only trait that was better explained by soil than by climate (Fig. 4d).

A central question in this research was whether the functional beta diversity at a given scale was higher or lower than that expected based on the observed species beta diversity. We tested

this using a null model that accounted for the potential effects of dispersal limitation by fixing the observed spatial distributions of species. Deviations of the observed functional beta-diversity values from the null expectations therefore indicate the influence of deterministic assembly processes (Swenson *et al.*, 2011). We found that, when accounting for multiple traits, functional beta diversity was lower than expected at fine spatial scales ( $< 600$  km) and higher than expected at broad spatial scales ( $> 1800$  km; Fig. 5a). The lower than expected functional beta diversity at fine scales provides evidence that functional composition converges in plots sharing similar environments due to environmental filtering (Smith & Wilson, 2002). Interestingly, functional convergence occurred despite the generally high species turnover between plots (Fig. 3a), highlighting the potential disconnect between species and functional beta diversity (Fukami *et al.*, 2005). The higher than expected functional beta diversity at broad spatial scales is consistent with strong, deterministic changes in functional composition across environmental gradients (Wright *et al.*, 2005; Moles & Westoby, 2006; Swenson & Enquist, 2007; Moles *et al.*, 2009). Turnover in species composition was often complete at these distances (Fig. 3a), but stochastic species turnover resulting from dispersal limitation alone could not account for the observed levels of functional beta diversity. Rather, such large, directional changes in functional composition are expected if the traits being measured relate to broad-scale abiotic gradients, as has been previously shown in this system (Swenson & Weiser, 2010).



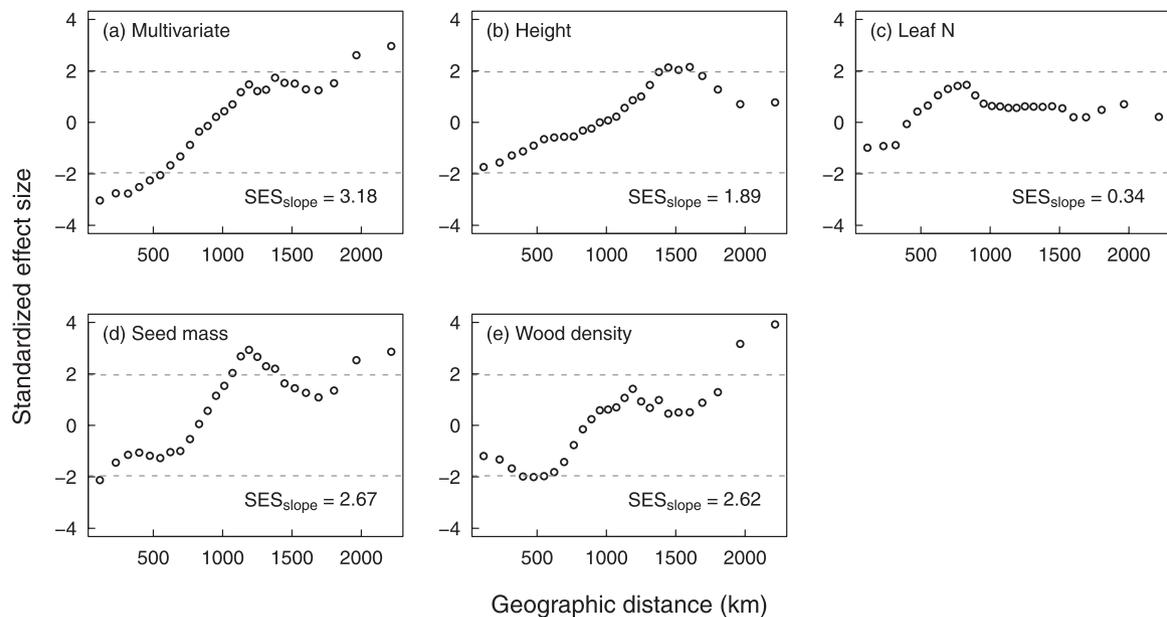
**Figure 4** Variance partitioning results. Venn diagrams show the partitioning of among-plot variation in (a) species composition, (b) functional traits, (c) maximum height, (d) leaf nitrogen content, (e) seed mass, and (f) wood density, among three sets of explanatory variables: spatial (principal coordinates of neighbour matrices), edaphic and climatic. The reported values are adjusted  $R^2$  statistics, representing the proportion of variation explained by a given component. Italics indicate statistically significant components ( $\alpha = 0.05$ ). Significance of shared components could not be tested due to a lack of degrees of freedom.

Despite the observed non-random levels of functional beta diversity at fine and broad scales, the functional beta diversity between forest plots separated by approximately 600–1800 km was generally not significantly different from the null expectation (Fig. 5a). This does not, however, necessarily imply an absence of niche-based processes at these scales. The null expectations were based on observed patterns of species beta diversity, which were probably driven in part by niche-based processes. Our null model was therefore not a purely ‘neutral’ model and should be considered a conservative test of niche-based processes. In addition, at intermediate scales there was a wide range of environmental similarities between plots, leading to instances of both functional convergence and divergence. Our analysis averaged the between-plot similarities found at each distance, leading to intermediate levels of mean functional beta diversity at intermediate scales. Nevertheless, the directional change in the standardized effect sizes along the geographic distance gradient (Fig. 5a) demonstrates an overall shift from functional convergence between plots at fine scales to functional divergence between plots at broad scales, supporting our initial hypothesis.

The general trends from null model analyses using individual traits were similar to those found using multivariate functional

beta diversity with a few exceptions (Fig. 5b–e). First, no individual trait had lower than expected turnover except at the very smallest distances. This finding demonstrates that trait-based filtering on local abiotic gradients is more easily detected when considering multiple axes of function rather than just one. Second, the general increase in standardized effect sizes with geographic distance was not evident for leaf nitrogen (Fig. 5c). Previous work in this system has demonstrated that the geographic distribution of leaf nitrogen is complex. In particular, the other traits tend to change predictably from north to south in eastern North America, while community mean leaf nitrogen peaks at mid-latitudes (Swenson & Weiser, 2010). The unimodal distribution of leaf nitrogen with latitude is not expected to produce a simple linear distance decay in similarity.

Another interesting result of the null model analysis was that the overall rate of distance decay of functional similarity (measured as the slope of the relationship between functional beta diversity and geographic distance) was greater than expected based on species turnover (Fig. 5a). Consistent with this finding, functional beta diversity had much stronger spatial structure than species beta diversity (Fig. 3a, b). Species beta diversity was high even at the smallest scales and, compared with functional beta diversity, increased relatively little with increasing distance.



**Figure 5** Results of null model analyses of functional beta diversity in relation to geographic distance for forest plots in the eastern United States. Data are presented as standardized effect sizes (SES). SES values above 1.96 (upper dashed line) indicate significantly higher functional beta diversity than expected given the observed species beta diversity. SES values below  $-1.96$  (lower dashed line) indicate significantly lower functional beta diversity than expected given the observed species beta diversity.  $SES_{slope}$  indicates the deviation of the slope of the relationship between observed functional beta diversity and geographic distance from the null expectation. Positive values indicate faster than expected distance decay of functional similarity.

A possible explanation for this difference in spatial structure is that species turnover was driven by fine-grained environmental variation (i.e. edaphic variables), and functional turnover was driven by coarse-grained climatic variation. This is unlikely, as both species and functional beta diversity were most strongly related to climate (Fig. 4a, b). A more probable explanation is that species beta diversity was high at fine scales due to priority effects and ecological drift among functionally similar species (Fukami *et al.*, 2005). Niche-based and neutral processes act simultaneously to structure communities (Chave, 2004; Adler *et al.*, 2007), and our results support the view that species composition is more strongly influenced by neutral processes than functional composition (Chase & Myers, 2011; Swenson *et al.*, 2012).

Our finding of deterministic turnover in functional composition across a broad geographic gradient complements recent work examining patterns of functional turnover across local scale gradients and through time. Swenson *et al.* (2011) found that functional turnover was faster than expected based on levels of species turnover across an elevational gradient in tropical tree communities. Similarly, Swenson *et al.* (2012) found higher than expected functional turnover through time in tropical forests undergoing rapid changes in environmental conditions following disturbance, but lower than expected functional turnover in late successional forests with relatively constant environments. Fukami *et al.* (2005) also found that functional composition converged more strongly than expected through time in environmentally homogeneous experimental grassland communities. Together with the results of the present study, a common

pattern emerges: for a given level of species turnover, functional beta diversity will be lower than expected if the environment remains constant (in space or time) and higher than expected if the environment changes rapidly. These patterns of functional beta diversity reveal signals of deterministic assembly processes that are not evident from patterns of species beta diversity alone.

### Limitations

The present work study has a few key limitations that we would like to point out. First, the analysis included four functional traits, selected because they reflect distinct axes of functional variation and are widely available for the tree flora of eastern North America. As data for additional traits become available, similar analyses should be conducted to determine if distinct trait sets produce different functional beta-diversity patterns. Second, based on the availability of data, we defined species functional strategies using mean trait values. Our analysis therefore accounted for interspecific but not intraspecific trait variation. Intraspecific variation may account for a large proportion of community-level shifts in trait values across environmental gradients (Cornwell & Ackerly, 2009; Jung *et al.*, 2010), although the relative importance of intraspecific variation is expected to decrease at very broad spatial scales (Albert *et al.*, 2011). We nevertheless expect that including intraspecific variation in the analysis of functional beta-diversity patterns will strengthen the signals of deterministic community assembly processes. Finally, the small size of forest plots analysed in this study probably increased the stochastic variation in community composition

between plots (Chase, 2003; Chase & Myers, 2011), contributing to high overall levels of beta diversity. Using a larger sampling grain size may have increased our ability to detect spatial beta-diversity patterns (Nekola & White, 1999).

## CONCLUSIONS

Investigating functional beta-diversity patterns has recently emerged as a useful tool for disentangling the roles of niche-based and neutral community assembly processes. This study represents, to our knowledge, the first analysis of functional beta diversity across broad-scale geographic and environmental gradients. We show that functional beta-diversity patterns in tree communities of eastern North America could not have been generated by neutral processes, such as dispersal limitation and ecological drift, alone. These results support a model of community assembly driven by the deterministic filtering of species based on their functional traits across environmental gradients.

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## SUPPORTING INFORMATION

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

**Appendix S1** Results of forward selection of explanatory variables.

## BIOSKETCH

**Andrew Siefert** is a PhD student at Syracuse University. He has interests in plant community assembly and functional ecology.

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