*Running head: Species-pool functional diversity*

Inferring community assembly mechanisms across biogeographic regions:

the importance of species-pool functional diversity

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**Abstract (150/150 words)**

Species-pool functional diversity is a largely unexplored dimension of regional species pools that may influence community-assembly and spatial variation in community composition (β-diversity). We examined patterns of functional β-diversity across three temperate forests predicted to vary in species pool functional diversity – a western coniferous forest; a central deciduous forest; and an eastern deciduous forest – and examined how environmental heterogeneity (soil and topography) and species pool functional diversity (leaf, stem, and seed traits) may jointly influence patterns of β-diversity. Our results suggest that species-pool functional diversity and environmental heterogeneity interact in such a way that high species-pool functional diversity may enhance β-diversity when environmental heterogeneity is low, and that low species-pool functional diversity may suppress β-diversity when environmental heterogeneity is high. Consequently, species-pool functional diversity may be an important driver of spatial variation in biodiversity and our results suggest that environmental heterogeneity alone cannot explain variation in β-diversity among biogeographic regions.

**Keywords**: beta-diversity; community assembly; diversity gradients; environmental heterogeneity; functional biogeography; functional diversity; plant functional traits; regional species pool; species sorting

**Introduction**

A key goal in ecology is to determine how multiple processes at different scales influence patterns of biodiversity. Variation in biodiversity can arise from smaller-scale mechanisms of community assembly such as competition and environmental filtering as well as from larger-scale processes such as dispersal and speciation ([Vellend 2010](#_ENREF_47)). To quantify the relative importance of community assembly mechanisms at different scales, ecologists often examine patterns of spatial variation in community composition – β-diversity ([Whittaker 1960](#_ENREF_49); [Anderson *et al.* 2011](#_ENREF_2)). Recently, studies have expanded this focus on β-diversity to quantify functional trait variation among communities (functional β-diversity) to infer the relative importance of different drivers of community assembly (e.g., [Swenson *et al.* 2011](#_ENREF_46); [Siefert *et al.* 2013](#_ENREF_41); [Spasojevic *et al.* 2014a](#_ENREF_42)). Much of the research in this area has focused on understanding the relative importance of niche selection (abiotic or biotic factors), dispersal, and ecological drift in driving patterns of β-diversity. For example, a classical explanation for variation in β-diversity among sites in different regions is that β-diversity is driven by geographic differences in environmental conditions ([Whittaker 1960](#_ENREF_49); [Qian & Ricklefs 2007](#_ENREF_35)). In this case, functional β-diversity is predicted to be higher in regions with greater environmental heterogeneity and lower in regions in more homogenous environments ([Questad & Foster 2008](#_ENREF_36)). Likewise, variation in β-diversity among sites in different regions may be influenced by geographic differences in dispersal limitation ([Qian & Ricklefs 2007](#_ENREF_35)). For example, species with low dispersal ability (e.g., gravity-dispersed seeds) can have higher β-diversity than species with high dispersal ability (e.g., wind-dispersed seeds) ([Nekola & White 1999](#_ENREF_28)). However, a growing body of research suggests that community assembly and the resulting patterns of β-diversity may also be influenced by the biogeographic processes (speciation, extinction, immigration) that create variation among the regional species pools from which communities assemble ([Kraft *et al.* 2011](#_ENREF_19); [Lessard *et al.* 2012](#_ENREF_24); [Cornell & Harrison 2014](#_ENREF_8); [Zobel 2016](#_ENREF_50)).

To date, the extent to which the assembly of communities across sites in different biogeographic regions is driven by niche selection, ecological drift, dispersal, biogeographic processes or the interplay among these factors, remains largely unresolved ([Lessard *et al.* 2012](#_ENREF_24); [Qian *et al.* 2013](#_ENREF_34)). Research focused on γ-diversity – the size of the regional species pool from which communities assemble – has provided important biogeographic insights for understanding patterns of β-diversity ([Kraft *et al.* 2011](#_ENREF_19); [Cornell & Harrison 2014](#_ENREF_8)). For example, communities assembled from a larger species pool may be more likely to have higher β-diversity than communities assembled from a smaller species pool simply owing to random sampling effects (Kraft et al. 2011, Myers et al. 2013) or because larger species pools increase the likelihood that colonization history influences community composition (i.e., priority effects; Chase 2003). Although the influence of γ-diversity on patterns of biodiversity has been a major focus of community ecology for decades ([Ricklefs 1987](#_ENREF_40); [Cornell & Harrison 2014](#_ENREF_8)), studies of γ-diversity have not considered that species pools potentially contain many species with functionally-redundant traits.

Species-pool functional diversity (SPFD) – the functional diversity of the species occurring in a particular region that can potentially inhabit a site because of suitable local ecological conditions ([modified from Zobel 2016](#_ENREF_50)) – may strongly influence community assembly and patterns of β-diversity. In Fig. 1, we illustrate this idea using a simple conceptual example for two hypothetical biogeographic regions, one with low SPFD (Fig 1a) and one with high SPFD (Fig. 1b), where γ-diversity (11 species), dispersal, and environmental heterogeneity (niche selection) are identical. If environmental heterogeneity is equally high among communities within the two regions. Low SPFD may “suppress” functional β-diversity by constraining niche selection for dissimilar traits among communities that vary in environmental conditions, resulting in empty niches. Simply put, the species that could fill a given “empty” niche are not in the species pool due to extinction, or a lack of speciation or immigration into the regional pool (Fig. 1a). In contrast, high SPFD may "boost" functional β-diversity by increasing selection for dissimilar traits among communities that vary in environmental conditions, resulting in more-complete filling of niche space and stronger species sorting across environmental gradients (Fig. 1b; [Questad & Foster 2008](#_ENREF_36); [Siefert *et al.* 2013](#_ENREF_41)). Simply put, speciation or immigration have resulted in a functionally diverse pool of species and can potentially fill more of the available niche space in the community. In contrast, if environmental heterogeneity is equally low in the two regions, low SPFD may also suppress functional β-diversity via weak species sorting across environmental gradients (Fig. 1a), but high SPFD may boost functional β-diversity via dispersal (Fig. 1b). For example, dispersal of individuals from a functionally-diverse species pool could maintain species in in sub-optimal habitats through source-sink dynamics (i.e., mass effects; Leibold et al. 2004), resulting in higher functional β-diversity than expected based on the degree of environmental heterogeneity. Finally, low SPFD may suppress functional β-diversity by increasing opportunities for colonization history (historical contingencies) to create priority effects ([Fukami *et al.* 2005](#_ENREF_14)). Our simplified example in Fig. 1 highlights potential influences of SPFD on community assembly in regions where environmental heterogeneity is either high or low. In real-world communities, however, both SPFD and environmental heterogeneity likely differ among biogeographic regions.

We explored this conceptual framework by comparing drivers of functional β-diversity among three large, stem-mapped temperate forest plots distributed across different biogeographic regions of North America (Table 1). We compared patterns of observed functional β-diversity of six plant functional traits (leaf area, specific leaf area, leaf water content, wood density, bark thickness, seed mass) across soil-resource and topographic gradients in each plot. We used variation-partitioning to determine the amount of variation in β-diversity explained by environmental heterogeneity, spatial variables, and unmeasured factors ([Legendre *et al.* 2009](#_ENREF_22); [Myers *et al.* 2013](#_ENREF_27)) and additionally used a null-model to examine the influence of SPFD in the in the absence of local assembly processes. We found that high SPFD may enhance β-diversity when environmental heterogeneity is low and that low SPFD may suppress β-diversity when environmental heterogeneity is high. These results suggest that SPFD may be a key, but underappreciated, driver of spatial variation in biodiversity.

**Methods**

*Study Sites*. Our three study sites (Table 1) are part of a global network of forest-ecology plots monitored through the Smithsonian Center for Tropical Forest Science and Global Forest Earth Observatory ([CTFS-ForestGEO; Anderson-Teixeira *et al.* 2015](#_ENREF_1)). The Wind River Forest Dynamics Plot (WFDP) is a 25.6 ha (800 x 320m) forest-dynamics plot containing 22 species and located in a Douglas fir-western hemlock dominated coniferous forest in southwestern Washington (USA; 45.8197 N, -121.9558 W; mean annual temperature 16.8 °C; mean annual precipitation 2493 mm). Additional information about the Wind River forest dynamics plot is available in Lutz et al. ([2013](#_ENREF_25)). The Tyson Research Center Plot (Tyson) is a 25-ha (500 x 500 m) forest-dynamics plot containing 42 species and is located in an oak-hickory dominated deciduous forest on the northeastern edge of the Missouri Ozarks (USA; 38.5178 N, -90.5575 W; mean annual temperature 13.5 °C; mean annual precipitation 957 mm). For this study, we use data from a 20-ha section of the Tyson plot that was censused from 2011-2014. Additional information about Tyson is available in Spasojevic *et al.* ([2014b](#_ENREF_44)). The Smithsonian Environmental Research Center (SERC) plot is a 16-ha (400 x 400 m) forest dynamics plot containing 67 species and is located in a poplar-elm-ash-sycamore dominated deciduous forest in Maryland (USA; 38.8891 N, -121.9958 W; mean annual temperature 14.1 °C; mean annual precipitation 1128 mm). Additional information about SERC is available in McMahon & Parker ([2015](#_ENREF_26)). At all three sites, all free-standing stems of woody species greater than 1 cm diameter at breast height (dbh) have been identified, tagged, measured and mapped following CTFS-ForestGEO protocols ([Condit 1998](#_ENREF_7)). Each forest plot is subdivided into 20 x 20 m quadrats (Wind River: N=640, Tyson: N=504, SERC: N=399) that represent local communities.

*Environmental heterogeneity*. To quantify differences in environmental heterogeneity among sites we measured 13 soil variables and 4 topographic variables. Following the sampling design described in John *et al*. ([2007](#_ENREF_18)), we measured spatial variation in available nitrogen (N), base saturation, effective cation exchange capacity (ECEC), exchangeable cations (Al, Ca, Fe, K, Mg, Mn, Na), pH, plant-available phosphorous (P), and total exchangeable bases (TEB) at each site . Details on soil sampling methods can found in Spasojevic et al. ([2014b](#_ENREF_44)). Quadrat level estimates of each soil variable were derived from kriged values using the geoR package ([Ribeiro & Diggle 2001](#_ENREF_39)) in R ([R Core Team 2014](#_ENREF_37)). All soil analyses were performed at the Soils Laboratory at the Smithsonian Tropical Research Institute, Panama (http://stri.si.edu/sites/soil/).

For each 20 x 20 m quadrat, we calculated aspect, convexity, mean elevation, and slope. Mean elevation above sea level was quantified as the mean elevation of the four corners of each quadrat. Slope and aspect were quantified using the slope and aspect tools in ArcGIS 10.1. Aspect was measured as the direction of the steepest slope within each quadrat. Because aspect is a circular variable, we used both sin(aspect) and cosine(aspect) in our analyses ([Legendre *et al.* 2009](#_ENREF_22)). Convexity was measured as the elevation of a given quadrat minus the mean elevation of the eight surrounding quadrats ([Legendre *et al.* 2009](#_ENREF_22)). For the edge cells, convexity was measured as the elevation of the center point minus the mean of the four corners ([Legendre *et al.* 2009](#_ENREF_22)).

*Trait sampling*

To describe SPFD and patterns of functional β-diversity, we measured six key plant functional traits at each site: leaf area, specific leaf area (SLA), leaf water content (LWC), wood density, bark thickness, and seed mass. Leaf area is associated with leaf energy and water balance, where small leaf size represents a strategy to cope with heat stress, drought stress, cold stress and photo-oxidative stress ([Perez-Harguindeguy *et al.* 2013](#_ENREF_33)). Specific leaf area is associated with resource uptake strategy and tissue N, where high SLA represents a strategy to maximize carbon gain and relative growth rate ([Reich *et al.* 1997](#_ENREF_38)). Leaf water content is associated with relative growth rate ([Garnier & Laurent 1994](#_ENREF_16)) and tolerance to low water availability ([Farooq *et al.* 2009](#_ENREF_13)). Wood density is associated with mortality rate, hydraulic lift and the relative mechanical strength of the plant ([Enquist *et al.* 1999](#_ENREF_12)). Bark thickness is associated with protection against biotic and abiotic threats and respiration ([Paine *et al.* 2010](#_ENREF_31)). Seed mass is related to dispersal ability and a reproductive strategy where species that produce few large seeds are thought to be better competitors and those that produce many small seeds are thought to be better dispersers ([Cadotte 2007](#_ENREF_6)). Trait collection followed protocols outlined in Perez-Harguindeguy *et al.* ([2013](#_ENREF_33)) - see Appendix S1 for details.

*Statistical analysis and Null modeling*. To describe variation in environmental heterogeneity among sites we first used a principle components analysis (PCA) to visualize the scatter of quadrats in environmental space. Principle component analysis was conducted using the prcomp function in the R ([R Core Team 2014](#_ENREF_37)) and all environmental variables were scaled. We then used a multivariate test of homogeneity of dispersion ([Anderson *et al.* 2006](#_ENREF_3)) based on scaled Euclidean distances for all environmental variables to test if each site differed in their distance-to-centroid values in environmental space using the ‘betadisper’ function in the R vegan package ([Oksanen *et al.* 2010](#_ENREF_29)). We tested for significance using a permutation test with 999 runs using the ‘permutest’ function in the R vegan package ([Oksanen *et al.* 2010](#_ENREF_29)).

To quantify species pool functional diversity (SPFD) among sites we calculated the multivariate functional dispersion (FDis) of all species present at each site weighted by their overall abundance within the whole forest dynamics plot. In multidimensional trait space, FDis is the mean distance of each species, weighted by relative abundances, to the centroid of trait space for all species in the community ([Laliberte & Legendre 2010](#_ENREF_20)). Functional diversity calculations were conducted using the FD package ([Laliberte & Legendre 2010](#_ENREF_20)) in R ([R Core Team 2014](#_ENREF_37)).

We calculated observed functional β-diversity at each site as the dissimilarity among quadrats in scaled community weighted mean (CWM) trait values. For each quadrat we calculated CWM trait values as the sum across all species of species’ trait values weighted by their relative abundance ([Garnier *et al.* 2004](#_ENREF_15)). Observed β-diversity is the average distance-to-centroid, measured as the average Euclidean distance from an individual quadrat to the centroid of the group of all quadrats in trait space, and was calculated using the ‘betadisper’ function in the R vegan package ([Oksanen *et al.* 2010](#_ENREF_29)). For simplicity, we focus here on overall patterns of multivariate functional composition calculated using all six traits combined, rather than separate patterns for each individual trait. Although this approach may obscure the functional response of individual traits ([Spasojevic & Suding 2012](#_ENREF_43)), it provides insights into how the overall functional composition of communities may be influenced by SPFD and allows us to more simply present our conceptual framework (Fig. 1). We include patterns of β-diversity for individual traits in supplementary Fig. S2.

To explore the influence of SPFD on patterns of functional β-diversity in the absence of local assembly mechanisms, we used a null-model approach that simulates random assembly of local communities from the regional species pool at each site. We first defined the species pool as the total number of species and the total abundance of each species observed across each plot. We then simulated functional composition 9999 times in each quadrat by randomly sampling individuals from the regional species pool while preserving the relative abundance of each species in the regional pool and the total number of individuals in each plot and recalculating CWM trait values for each quadrat ([Spasojevic *et al.* 2014a](#_ENREF_42)). We then tested for differences among sites in observed β-diversity and expected β-diversity using a nonparametric analysis of variance based on distance-to-centroid values ([Anderson *et al.* 2011](#_ENREF_2)).

To explore the relative importance of different assembly mechanisms, we compared the extent to which observed functional β-diversity was explained by environmental variables (described above) and spatial variables using distance-based redundancy analysis (dbRDA; [Peres-Neto *et al.* 2006](#_ENREF_32); [Legendre *et al.* 2009](#_ENREF_22)) at each site. Spatial variables included spatial eigenvectors (see Appendix S2) obtained from Principal Components of Neighbor Matrices (PCNM) which describe spatial structure among quadrats ([Borcard & Legendre 2002](#_ENREF_5)). Following Blanchet et al. ([2008](#_ENREF_4)), we used dbRDA to partition variation in β-diversity into individual fractions explained by pure (spatially-unstructured) environmental variables, spatially-structured environmental variables, and spatial variables. We then performed forward-model selection using the ‘Forward.sel’ function in the R packfor package ([Dray *et al.* 2007](#_ENREF_11)). Environmental and spatial variables retained after forward-model selection (see Appendix S2) were used to partition variation in functional β-diversity into the individual fractions listed above. Finally, we tested for differences among sites in the total variance explained, the fraction explained by environmental variables and the fraction explained by spatial variables using bootstrap tests ([Peres-Neto *et al.* 2006](#_ENREF_32)) based on 999 iterations.

**Results**

Environmental heterogeneity (distance-to-centroid) varied among the three sites (Fig. 2a; F2,1540=721.7, P<0.01) with SERC having the greatest environmental heterogeneity, Tyson having intermediate, and Wind River having the least (Fig. S1). Species pool functional diversity also varied among sites (Fig. 2b) with Wind River having the highest SPFD (FDis = 1.93), SERC having intermediate (FDis = 1.60), and Tyson having the lowest (FDis = 1.29).

Observed functional β-diversity was highest at SERC, intermediate at Tyson, and lowest and Wind River (Fig. 3a; homogeneity of multivariate dispersion test on average distance to centroids, F2,1540=19.67, P<0.01) correlating with environmental heterogeneity. Tukey HSD pairwise comparisons revealed that all three sites significantly differ from each other (Wind River – Tyson: P=0.049; Wind River – SERC: P<0.01; Tyson – SERC: P<0.01). In contrast, expected β-diversity was highest in Wind River, intermediate at SERC, and lowest at Tyson (Fig. 3b; F2,1540=18.54, P<0.01) correlating with SPFD. Tukey HSD pairwise comparisons revealed that all three sites significantly differ from each other (Wind River – Tyson: P<0.001; Wind River – SERC: P<0.01; Tyson – SERC: P<0.01).

To disentangle whether patterns of β-diversity may have resulted from dispersal limitation, environmental filtering or a combination of both, we examined the extent to which the total amount of variation in β-diversity explained by environmental and spatial gradients varied among sites. The amount of observed β-diversity explained by the environment (both pure environmental and spatial structured environmental variables) significantly differed among sites (bootstrap test of environmental fractions P<0.01, Fig. 4a) with the environment explaining the most at Tyson (67.5%) and SERC (59.7%) and the least at Wind River (22.5%). Pure spatial processes also differed among site (bootstrap test of spatial fractions P<0.01, Fig. 4a) and explained more at Wind River (34.4%) than at either Tyson (14.8%) or SERC (19.2%). Lastly, the portion of unexplained variation in observed β-diversity was over twice as high at Wind River (43.1%) than at either Tyson (19.4%) or SERC (21.1%).

**Discussion**

Functional β-diversity patterns are increasingly being used to understand the relative importance of niche selection, dispersal and ecological drift in community assembly (e.g., [Swenson *et al.* 2011](#_ENREF_46); [Siefert *et al.* 2013](#_ENREF_41); [Spasojevic *et al.* 2014a](#_ENREF_42)). While we found evidence for these processes contributing to patterns of functional β-diversity at all three sites, our results also suggest that the relative importance of these processes was mediated by the functional diversity of the pool of species from which these communities assembled. Specifically, we found smaller differences in functional β-diversity among sites than what we would have predict based on the relatively large differences in environmental heterogeneity among sites. Based on the framework we propose here (Fig. 1), our results suggest that functional β-diversity may have been enhanced by high SPFD in the forest with low environmental heterogeneity and suppressed by low SPFD in the forests with high environmental heterogeneity. Our results suggest that the functional diversity of the regional species pool may be a critical, yet overlooked, driver of variation in β-diversity among biogeographic regions.

Comparisons of β-diversity across biogeographic regions may be strongly influenced by the degree of environmental heterogeneity within regions. For example, De Caceres *et al.* ([2012](#_ENREF_10)) found that β-diversity among tree communities may be positively correlated with topographic heterogeneity. When we examined patterns of observed functional β-diversity, without considering SPFD, we found a similar pattern – functional β-diversity was highest at SERC, where environmental heterogeneity was highest and lowest at Wind River where environmental heterogeneity was lowest. Based on these patterns alone, we would assume that species sorting along environmental gradients (niche selection as a mechanism of community assembly) is stronger at SERC and Tyson and weaker at Wind River. However, the difference in functional β-diversity among Tyson and Wind River, though statistically significant, is much smaller than what would be expected based on the differences among those sites in environmental heterogeneity. Moreover, we found that environmental variables explained the largest amount of the variation in β-diversity at Tyson, where environmental heterogeneity is intermediate (Fig. 4a). Together, these results suggest that environmental heterogeneity may not be the only driver of functional β-diversity and that other processes likely contribute.

In addition to the variation in environmental heterogeneity among sites, we also found that SPFD significantly differed among sites, with the highest SPFD in Wind River, intermediate at SERC and the lowest and Tyson. Interestingly, this pattern did not correlate with γ-diversity – γ-diversity was highest at SERC (67 species), intermediate at Tyson (42 species) and lowest at Wind River (22 species). While our approach of using whole plot species richness to estimate γ-diversity likely underestimates γ-diversity due to the influence of dark-diversity ([Paertel *et al.* 2011](#_ENREF_30)), we should be underestimating γ-diversity relatively equally at all sites and potentially less so at Wind River as it is the largest of the three forest plots. This lack of a correlation between γ-diversity and SPFD suggests speciation isn’t the only biogeographic processes we should consider in community assembly. While speciation is important for γ-diversity and community assembly ([Vellend 2010](#_ENREF_47)), extinction may also play a key role in shaping regional species pools ([Cowling & Lombard 2002](#_ENREF_9)) by removing species with particular functional strategies and thus altering SPFD. Consistent with this idea, many hardwood taxa found at Tyson and SERC (Hickories, Elms and Sycamores) were extinct from the Pacific Northwest by the late Pleistocene ([Waring & Franklin 1979](#_ENREF_48)) thus altering the functional diversity of the pool of species able to colonize Wind River; without this extinction, SPFD may have been even higher than currently observed at Wind River. Understanding what caused the variation in SPFD among our three sites is beyond the scope of our current research, but analyses mapping traits onto phylogenies at regional scales will likely help us understand the biogeographic drivers of SPFD.

Even though the three forests differed relatively greatly in environmental heterogeneity and SPFD (Fig. 2a and 2b), why doesn’t functional β-diversity differ more among these three forests? Our results suggest that SPFD and environmental heterogeneity interact in such a way that high SPFD may enhance β-diversity when environmental heterogeneity is low and that low SPFD may suppress β-diversity when environmental heterogeneity is high. Specifically, at Wind River we found that SPFD was high and environmental heterogeneity was low. Based on our conceptual framework, this pattern suggests that the high SPFD at Wind River may have “enhanced” β-diversity because the species with less available niche space across the landscape (due to the more homogenous environment) may have been maintained in sub-optimal habitats via dispersal ([e.g., source-sink dynamics; Leibold *et al.* 2004](#_ENREF_23)). This idea is supported by the two lines of evidence. First, observed functional β-diversity in seed mass (Fig, S2f) – a trait correlated with dispersal ability ([Cadotte 2007](#_ENREF_6)) – is very low at Wind River suggesting there is little variation in seed mass among local communities and that communities are less likely to be dispersal limited as all sizes of seeds (large and small) are in most all communities. Second, the amount of variation in functional β-diversity explained by spatial processes was highest at Wind River (Figs. 4a) – explaining almost twice as much of the variation in β-diversity than at either of the other two sites. This larger spatial fraction suggest that communities that are closer together have more similar trait composition than communities that are farther apart, irrespective of environmental conditions ([Legendre *et al.* 2009](#_ENREF_22)). Based on our framework, we suggest that this spatial aggregation reflects species in source habitats contributing functional traits to communities in nearby sink habitats and that this process may be happening for multiple species in different areas across this plot. Together, these patterns suggest that dispersal may be contributing more to β-diversity in this forest and SPFD may be “boosting” β-diversity beyond what would be expected based on environmental heterogeneity alone.

In contrast, at both Tyson and SERC we found that environmental heterogeneity was higher, and SPFD was lower. Based on our conceptual framework, this pattern suggests that this low SPFD may have “suppressed” β-diversity at these two sites because species that could potentially take advantage of the high environmental heterogeneity and partition the environment with the species currently in the species pool have not evolved (speciated) or immigrated into that species pool, resulting in empty niches. Supporting this idea, there are many quadrats (communities) at these two sites with relative low stem densities and low herbaceous cover suggesting potentially empty niche space. For example, at Tyson communities on ridge tops have higher maximum temperatures and have low species richness ([as few as 3 species; Spasojevic *et al.* 2014c](#_ENREF_45)) and low stem density (as low as 0.75 stems/m2; Spasojevic and Myers unpublished data) suggesting a potential empty niche for xeric, high temperature adapted species. Moreover, our variation partitioning results, where the amount of variation functional β-diversity explained by environmental factors was highest at Tyson and SERC (Fig. 4a), suggesting that niche selection is stronger at these sites and that these empty niches are likely not filled by dispersal and source sink dynamics.

*Conclusions and future directions*

In Vellend’s ([2010](#_ENREF_47)) conceptual synthesis of community ecology, he posited that there are four key processes that structure communities: niche selection, dispersal, ecological drift, and speciation. To date much of the research in trait-based community assembly has been focused on understanding the relative important of niche selection and ecological drift, with a smaller body of work focused on linking these two processes with dispersal. Our framework here (Fig. 1), is one of the first attempts to incorporate speciation (and other key biogeographic processes such as extinction and immigration which influence regional species pools) into such trait-based models of community assembly. Importantly, our framework suggests that when comparing community assembly mechanisms among sites in different biogeographic regions, accounting for the functional diversity among species in the regional species pool is critical for correctly inferring the processes of community assembly.

Importantly, the relationship between SPFD and γ-diversity remains untested and it is likely not as simple as a linear relationship between the size of the species pool and its functional diversity. For example, here we found that our site with the lowest γ-diversity had the highest SPFD. On the other hand Lamanna *et al.* ([2014](#_ENREF_21)) found that functional γ-richness exhibited a humped shaped relationship with latitude, suggesting a wider range of functional strategies at intermediate latitudes, where the size of the species pool is also intermediate. Determining the global relationship between SPFD and γ-diversity will be an important next step for understanding when SPFD is important for community assembly.

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**Tables**

Table 1. Characteristics of the three forest-dynamics plots.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Plot | Latitude | Longitude | Forest type  (dominant genera) | Plot size  (ha) | Elevation  range (m) | Number  of species1 | Number  of trees |
| Wind River,  Washington | 45.81 | -121.95 | Needle-leaf evergreen  (fir-hemlock) | 25.6 | 352–385 | 22 | 31,162 |
| Tyson Research Center,  Missouri | 38.51 | -90.55 | Broadleaf deciduous  (oak-hickory) | 20 | 172–233 | 42 | 31,800 |
| Smithsonian Environmental Research Center (SERC),  Maryland | 38.88 | -76.55 | Broadleaf deciduous  (tulip-poplar, oak, beech, ash, sycamore, elm) | 16 | 6–10 | 63 | 33,500 |

1Number of woody plants (excluding lianas) >1 cm diameter at breast height in censuses from 2011-2013 (Wind River), 2013 (Tyson), and 2008-2011 (SERC).

**Figures**

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Figure 1. Models of community assembly typically focus on the importance of dispersal, niche selection and ecological drift in structuring local communities. However, species pool functional diversity (SPFD) may mediate the influence of these processes. In this conceptual example two regions have similar size regional species pools (11 species), the relative strength of drift, dispersal, and niche selection are all similar, and the only difference among regions is in SPFD arising from biogeographic processes such as speciation, extinction and immigration. In the region where SPFD is low (A; similar colored species in the regional species pool) functional β-diversity (similar colors across all three pies on the right side of the figure) would be low, not necessarily due to a specific processes not being present, but because the low diversity in the regional species pool mediates those processes. In contrast, in the region where SPFD is high (B; different colored species in the regional species pool), greater functional diversity in the pool may increase opportunities for niche selection (abiotic and biotic filtering), resulting in increased functional β-diversity (different colors across all three pies on the right side of the figure). Thus, contrasting patterns of functional β-diversity among landscapes may, in part, be explained by variation in SPFD and its influence on community assembly mechanisms. Adapted from HilleRisLambers et al. ([2012](#_ENREF_17)).

Figure 2. Variation in (a) local environmental variables and (b) species pool functional diversity at each site. (a) Principle components analysis of the 18 environmental variables (13 soil variables and 5 topographic variables) measured in 20 x 20-m quadrats in Wind River (Orange; N = 640 quadrats), Tyson (Blue; N = 504 quadrats) and SERC (Green; N = 399 quadrats). Soil variables include aluminium (Al), calcium (Ca), base saturation (BS), effective cation exchange capacity (ECEC), iron (Fe), magnesium (Mg), manganese (Mn), pH, phosphorus (P), potassium (K), sodium (Na), total exchangeable bases (TEB), and total nitrogen (N). Topographic variables include convexity, eastern aspect (E aspect), elevation (elev), northern aspect (N aspect), and slope. (b) Principle coordinates analysis of the six plant functional traits (leaf area, specific leaf area, leaf water content, wood density, bark thickness, and seed mass) measured at each site. Species pool functional diversity was quantified as functional dispersion which calculates abundance weighted distance-to-centroids in principle coordinate trait space for all species at each site ([Laliberte & Legendre 2010](#_ENREF_20)). Size of points indicates relative abundance of each species at each site – larger circles are more abundant species.

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Figure 3. Variation in β-diversity among sites. (a) Observed functional β-diversity, and (b) expected functional β-diversity from a null model based on random sampling from the regional species pool. Boxes represent the median and 25th/75th percentile, and whiskers extend to 1.5 times the interquartile range. Boxes in (a) and (b) show median distance-to-centroid values of individual 20 x 20-m quadrats from the centroid of all quadrats at each site. Note the difference in the scale of the y-axis between panels (a) and (b).



Figure 4. Variation partitioning for observed functional β-diversity. The four partitions show the adjusted R2 values for environmental variables, spatially-structured environmental variables, spatial variables, and the unexplained variation based on distance-based redundancy analysis (see Appendix S1).