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EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Integrating species traits into species pools

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Abstract. Despite decades of research on the species-pool concept and the recent explosion of interest in trait-based frameworks in ecology and biogeography, surprisingly little is known about how spatial and temporal changes in species-pool functional diversity (SPFD) influence biodiversity and the processes underlying community assembly. Current trait-based frameworks focus primarily on community assembly from a static regional species pool, without considering how spatial or temporal variation in SPFD alters the relative importance of deterministic and stochastic assembly processes. Likewise, species-pool concepts primarily focus on how the number of species in the species pool influences local biodiversity. However, species pools with similar richness can vary substantially in functional-trait diversity, which can strongly influence community assembly and biodiversity responses to environmental change. Here, we integrate recent advances in community ecology, trait-based ecology, and biogeography to provide a more comprehensive framework that explicitly considers how variation in SPFD, among regions and within regions through time, influences the relative importance of community assembly processes and patterns of biodiversity. First, we provide a brief overview of the primary ecological and evolutionary processes that create differences in SPFD among regions and within regions through time. We then illustrate how SPFD may influence fundamental processes of local community assembly (dispersal, ecological drift, niche selection). Higher SPFD may increase the relative importance of deterministic community assembly when greater functional diversity in the species pool increases niche selection across environmental gradients. In contrast, lower SPFD may increase the relative importance of stochastic community assembly when high functional redundancy in the species pool increases the influence of dispersal history or ecological drift. Next, we outline experimental and observational approaches for testing the influence of SPFD on assembly processes and biodiversity. Finally, we highlight applications of this framework for restoration and conservation. This species-pool functional diversity framework has the potential to advance our understanding of how local- and regional-scale processes jointly influence patterns of biodiversity across biogeographic regions, changes in biodiversity within regions over time, and restoration outcomes and conservation efforts in ecosystems altered by environmental change.

Key words: biodiversity; biogeography; community assembly; conservation; dispersal; ecological drift; environmental change; functional traits; niche selection; regional species pools; restoration; species-pool functional diversity.

Introduction

A key challenge in ecology, biogeography, and conservation is to understand why multiple processes at different scales interact to determine patterns of biodiversity (Ricklefs 1987, Bond and Chase 2002, Chase and Myers 2011, Cornell and Harrison 2014, Brudvig et al. 2017). Trait-based community ecology and the regional species-pool concept have each provided a path toward understanding the causes of biodiversity within and across biogeographic regions, but have yet to be fully integrated with each other. Trait-based frameworks in community ecology have provided key insights into the relative roles of dispersal (the movement of individuals through space), ecological drift (changes in species relative abundances that are random

with respect to species identities), and niche selection (changes in species relative abundances due to abiotic and biotic conditions that give rise to deterministic fitness differences between species) in community assembly and species coexistence (e.g., Weiher and Keddy 1995, Weiher et al. 2011, HilleRisLambers et al. 2012, Spasojevic and Suding 2012, Adler et al. 2013, Kraft et al. 2015, Vellend 2016). At the same time, the regional species-pool concept has provided important insights into how speciation, extinction, and dispersal at larger spatiotemporal scales influence variation in local biodiversity (e.g., Ricklefs 1987, Eriksson 1993, Lessard et al. 2012*a*, Cornell and Harrison 2014, Zobel 2016). However, a key challenge is to integrate trait-based community ecology with the species-pool concept to understand why the relative importance of dispersal, ecological drift, and niche selection may vary within and among biogeographic regions (Questad and Foster 2008, Myers and Harms 2009*a*, de Bello et al. 2012, Violle et al. 2014).

Integrating trait-based community ecology with the species-pool concept has broad implications for understanding the extent to which theories in community ecology can be generalized across different biogeographic regions (Lawton 1999, Simberloff 2004, Ricklefs 2008), predict biodiversity responses to environmental change (Olden et al. 2004), and inform conservation and restoration of ecosystem functions (Funk et al. 2008, Laughlin 2014).

Despite the recent explosion of interest in both trait-based community assembly (Weiher et al. 2011, Mason and de Bello 2013, Violle et al. 2014, Kraft et al. 2015, Garnier et al. 2016) and the species-pool concept (Partel et al. 2011, Lessard et al. 2012a, Cornell and Harrison 2014, Mittelbach and Schemske 2015, Zobel 2016), surprisingly little is known about how changes in the functional diversity of species pools influence biodiversity and processes of community assembly. To date, trait-based frameworks (e.g., Weiher and Keddy 1995, Ackerly and Cornwell 2007, Funk et al. 2008, Gross et al. 2009, Spasojevic and Suding 2012, Laughlin 2014) have primarily focused on community assembly within a single biogeographic region from a regional species pool with a static composition of species or functional traits. On the other hand, the species-pool hypothesis suggests that local species diversity is determined by regional rather than local processes (Vellend 2016), but does not consider that the functional diversity of the regional pool may alter the relative importance of local processes. Additionally, species-pool concepts have focused primarily on patterns of taxonomic diversity, typically measured as the number of species in the regional pool (Zobel et al. 1998, Partel et al. 2011, Cornell and Harrison 2014). A limitation of these frameworks is that they do not make explicit a priori predictions for why or how changes in the functional diversity of regional species pools among biogeographic regions or within regions through time may alter the relative importance of different local community assembly processes (Questad and Foster 2008, Myers and Harms 2009b, Fukami 2015). Importantly, seemingly unpredictable patterns of biodiversity (e.g., "diversity anomalies"; Latham and Ricklefs 1993) may emerge among regions because species pools with similar richness may differ substantially in species-pool functional diversity (Myers and Harms 2009b, Swenson et al. 2011, Lessard et al. 2012b, Lamanna et al. 2014). Therefore, an integrative framework uniting recent advances in the species-pool concept and trait-based ecology has untapped potential to reveal why changes in the functional diversity of species pools within or among regions may alter local community assembly, patterns of biodiversity, and biodiversity responses to environmental change (Questad and Foster 2008, Myers and Harms 2009b, de Bello et al. 2012, Lamanna et al. 2014, Fukami 2015).

Here, we present a synthetic framework for understanding how and why a key but understudied component of regional species pools, species-pool functional diversity (SPFD), influences mechanisms of community assembly and patterns of biodiversity within and across biogeographic regions. First, we provide a brief overview of the ecological and evolutionary processes that give rise to differences in SPFD among regions and within regions over time. Second, we present predictions for how changes in SPFD across regions or within regions through time can influence the relative importance of different local community assembly processes that underlie patterns of biodiversity. Third, we outline experimental and observational approaches for empirical studies of SPFD. Last, we discuss applications of this framework to provide novel solutions for biodiversity conservation, environmental change biology, and restoration ecology.

What Causes Variation in Species-Pool Functional Diversity?

Differences in SPFD among regions can result from any process that adds or removes functionally redundant or functionally unique species to or from regional species pools. Importantly, these processes can lead to variable relationships between SPFD and the number of species in the regional species pool (species-pool richness). In some cases, SPFD may increase linearly with species-pool richness (Fig. 1, blue line), especially when additional species are functionally unique. For example, adaptive radiations (see *Speciation*) may result in a simultaneous increase in both species richness and functional diversity of species that occupy different niches in a region (Seehausen 2006). In other cases, SPFD may increase asymptotically (Fig. 1, yellow line) or show a hump-shaped relationship with species-pool richness, especially when additional species are functionally redundant. For example, studies of mammals at the global scale (Safi et al. 2011) and trees in eastern North America and Europe (Swenson et al. 2016) found that changes in multivariate functional diversity were asymptotically related to species richness at regional scales. Additionally, across tree assemblages spanning temperate and tropical latitudes, Lamanna et al. (2014) found a hump-shaped relationship between SPFD and absolute latitude, suggesting that SPFD and species-pool richness are decoupled. The decoupling of SPFD from species-pool richness suggests that changes in the taxonomic diversity of the regional species pool alone may not explain changes in biodiversity and community assembly within and across regions.

The decoupling of SPFD from species-pool richness may result from multiple non-mutually exclusive processes at different scales. These processes include biogeographic and/or historical processes (MacArthur and Wilson 1967, Donoghue 2008, Wiens et al. 2010, Weir and Price 2011), local-scale niche selection (Mittelbach and Schemske 2015), and large-scale anthropogenic and environmental changes (Olden et al. 2004, Laughlin 2014); each are the focus of a massive body of literature that cannot be completely summarized here. Instead, we provide an overview of key processes that can create differences in SPFD among regions and/or within regions over time. In particular, we focus on the processes that are relevant to short-term ecological dynamics that are the subject of most studies seeking to understand how local communities assemble and respond to environmental change (both across space and time).

Speciation

According to the species-pool hypothesis (Eriksson 1993, Zobel 1997), local species diversity is a product of the processes that determine regional species diversity, including
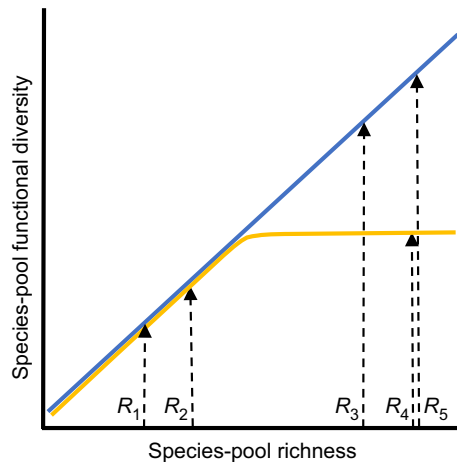
Fig. 1. Potential relationships between species-pool functional diversity (SPFD) and the number of species in the regional species pool (species-pool richness) among regions. Species-pool frameworks that focus on variation in species-pool richness among regions do not account for the fact that regions with species pools of similar size may be functionally similar or functionally dissimilar, or that regions with larger species pools may contain more functionally redundant species than regions with smaller species pools. In one case (blue line), SPFD increases linearly with species-pool richness among regions. In another case (yellow line), SPFD increases asymptotically with species-pool richness among regions, indicating a relatively high degree of functional redundancy in the regional pool of species-rich regions. When comparing regions R_1 and R_2, SPFD is directly proportional to species-pool richness, so that the region with the larger species pool has higher SPFD. However, when comparing regions R_3 and R_4, species-pool richness is a poor predictor of SPFD as functional redundancy in region R_4 results in lower SPFD than region R_3 even though species-pool richness is higher in region R_4. Similarly, R_4 and R_5 have the same species-pool richness (offset to improve visibility) yet differ greatly in SPFD due to greater functional redundancy in R_4.

speciation (Vellend 2016). A classic prediction of this hypothesis is that local species diversity should increase linearly with species-pool richness (Cornell and Harrison 2014). Empirical support for this prediction is mixed (Vellend 2016), but more importantly this prediction does not consider that different mechanisms of speciation can cause differences in SPFD among regions. For example, sympatric speciation can occur via polyploidy in plants (Levin 1975, Husband and Schemske 2000) and this can result in polyploids occupying distinct niches from their diploid progenitors (e.g., Laport et al. 2016, Ostevik et al. 2016). In such a case, speciation in one region may concurrently increase species pool richness and SPFD (Fig. 1, blue line). On the other hand, speciation is often allopatric with little niche differentiation (McPeek 1998, Turgeon et al. 2005). In this case, speciation may increase species pool richness but the influence on SPFD would depend on the degree of niche differentiation among sister species and may not increase SPFD (Fig. 1, yellow line) if sister species have similar niches (McPeek 1996, Price 2010, Weir and Price 2011). Speciation may be especially likely to create differences in SPFD among regions if one region undergoes an adaptive radiation (McPeek and Brown 2000). For example, rapid speciation of African cichlid fish (Seehausen 2006) greatly increased SPFD compared to regions that did not undergo the same

adaptive radiation. One key exception is when there is strong niche conservatism, the retention of niche-related ecological traits over time (Wiens et al. 2010), which has been found to impact local diversity (Partel 2002). For example, Harrison and Grace (2007) found that the positive productivity-richness relationship in the California flora was due to niche conservatism where a greater number of species in the region had evolved under high-productivity conditions and that this filtered down to affect local community composition. Therefore, regions with greater niche conservatism may have lower SPFD than regions with less niche conservatism because stronger niche conservatism constrains trait divergence among closely related species (Losos 2008).

Dispersal

Dispersal among regions (immigration and emigration) will influence differences in SPFD among regions depending on whether immigrants/emigrants are functionally unique or redundant (MacArthur and Wilson 1967, Petchey and Gaston 2006). For example, the immigration/introduction of exotic plant species into Germany has greatly reduced the functional diversity of ploidy level in the German Flora (Winter et al. 2008). Importantly, dispersal within a region may also influence differences in SPFD among regions. For example, dispersal within a region may promote regional coexistence of species through competition–colonization trade-offs (Amarasekare et al. 2004, Leibold et al. 2004) or counteracts extinction from local niche selection through mass effects (Leibold et al. 2004). If competition–colonization trade-offs or mass effects operate in one region, but not another, these differences may contribute to differences in SPFD among regions. Last, dispersal and speciation can also interact to determine variation in SPFD among regions; the order and timing of immigration can influence the extent of diversification during adaptive radiations. For example, experimental studies with bacteria have shown that early arrival of niche specialists can suppress diversification through increased competition (Fukami et al. 2007).

Ecological drift

Ecological drift is defined as changes in species relative abundances that are random with respect to species identities or functional traits (Vellend et al. 2014, Vellend 2016). Ecological drift is a key process in the Unified Neutral Theory of Biodiversity of Biogeography (Hubbell 2001), but is not synonymous with neutral theory because it does not include dispersal or speciation (which are separate processes). Similar to neutral theory, ecological drift influences community dynamics via random births and deaths (Chase 2007, Siepielski et al. 2010, Vellend et al. 2014, Gilbert and Levine 2017) and, thus, while ecological drift may cause differences in SPFD, it will have no *directional* influence on differences in SPFD among regions.

Niche selection

Abiotic conditions and/or biotic interactions will also influence differences in SPFD within a region over time or among region. Niche selection may decrease SPFD over

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time if abiotic conditions select for a narrower range of functional traits (Petchey and Gaston 2006). For example, Garcia-Morales et al. (2016) found that deforestation reduced the functional diversity of bats due to the local extinction of insectivorous bats. On the other hand, abiotic conditions may increase SPFD over time in other regions if niche section removes functionally redundant species (Fonseca and Ganade 2001). For example, Brandl et al. (2016) found that after the degradation of coral habitat by a tropical cyclone there was an increase in functional diversity of fish due to the loss of functionally redundant species. Importantly, differences in local environmental heterogeneity among regions (through space or time) may also influence differences in SPFD among regions. For example, spatial variation in soil resources may select for different traits in different local environments within a region, thereby increasing SPFD in regions with greater environmental heterogeneity (Harrison et al. 2006). Similarly, there is a well-documented link between rainfall and temporal variation in plant composition in California grasslands (Hobbs and Mooney 1995, Zavaleta et al. 2003, Dudney et al. 2017), where SPFD is likely increased by different groups specializing on different temporal environments (grasses in wet years and forbs in dry years). It is important to note that environmental heterogeneity and SPFD may not always be positively related due to processes such as niche conservatism. Finally, variation in biotic interactions among regions can also influence differences in SPFD. For example, competition for niche space has been found to limit niche differentiation in Himalayan song birds (Price et al. 2014), suggesting biotic niche selection may limit SPFD in some regions. Lastly, LaManna et al. (2017) found that the strength of conspecific negative density dependence was stronger for trees in the tropics than in the temperate zone suggesting that biotic interactions may influence SPFD through local scale coexistence mechanisms.

In summary, differences in SPFD among regions or within a region over time can arise from any of these four non-mutually exclusive processes that can interact through both space and time. While we have touched on how these processes interact, the specifics of how these processes interact to influence SPFD is still an open question that has rarely been explored (but see Lamanna et al. 2014, Violle et al. 2014) and is beyond the scope of this paper (see Future Directions question 3). Importantly, regardless of how these processes interact to create differences in SPFD, variation in SPFD among regions or within a region over time has great potential to influence differences in community assembly and local-scale patterns of biodiversity as well as efforts to restore communities in response to environmental change.

A Framework for Integrating Species-Pool Functional Diversity, Biogeography and Community Assembly

Just as trait variation in populations provides the template for natural selection in evolutionary biology (Darwin 1859), the diversity of functional traits within a regional species pool provides the template for niche selection in ecological communities (Shipley 2010). This concept is central to frameworks for trait-based community assembly, where the composition of local communities reflects the outcome of abiotic and biotic filtering of traits from the species pool (Zobel 2016). For example, if trait dissimilarity among species in local communities is smaller or larger than expected given the trait diversity of species in the regional pool, abiotic filtering or local biotic interactions are inferred to be important determinants of community assembly (Weiher and Keddy 1995, Weiher et al. 2011, de Bello et al. 2012). While these frameworks provide important insights into how communities assemble from a regional species pool with a static composition of species or traits, they do not provide explicit predictions for how changes in SPFD within or among regions influence the relative importance of community assembly mechanisms, patterns of biodiversity, and biodiversity responses to environmental change.

We hypothesize that differences in SPFD across biogeographic regions and temporal changes in SPFD within regions influence the relative importance of community assembly mechanisms. We illustrate this hypothesis using a simplified example of two hypothetical biogeographic regions that have identical species-pool richness, phylogenetic relatedness among species, dispersal, and variation in environmental conditions, but differ *only* in SPFD (Fig. 2). In the real world, all of these factors may vary among regions but, for illustrative purposes, we keep them constant to highlight the influence of SPFD.

In regions with high SPFD, niche selection should have a relatively stronger influence on community assembly (Fig. 2A). Higher SPFD should increase the likelihood that the regional species pool contains traits that confer fitness advantages in different environments and thereby increase opportunities for species to sort across local communities that differ in abiotic and biotic conditions. This prediction is based on metacommunity theory, which predicts that species sorting increases variation in community composition (β-diversity) across environmental gradients (Chase and Myers 2011), decreases the range or variance of trait values among co-occurring species in local communities relative to random assembly from the regional species pool (Weiher and Keddy 1995), and increases correlations between community-level trait values and environmental conditions across space (Cornwell and Ackerly 2009, Spasojevic et al. 2014a, Vellend 2016). Thus, higher SPFD should generally increase variation in trait composition among local communities (i.e., functional β-diversity) and strengthen relationships between community composition and the environment (Fig. 2A). Although few studies have tested these predictions, experimental studies in plant communities suggest that changes in SPFD have strong influences on community assembly. In a prairie grassland, Questad and Foster (2008) found that plant β-diversity increased when communities were assembled from an experimental species pool that contained more functional groups (i.e., grasses and forbs; analogous to high SPFD) compared to an experimental species pool that contained fewer functional groups (i.e., only grasses; analogous to low SPFD). Moreover, in a meta-analysis of seed-addition experiments, Myers and Harms (2009b) found seed arrival increased plant species richness more in experiments where the pool of added seeds had greater functional diversity (variation in seed size).

In regions with low SPFD, in contrast, certain traits are more likely to be absent from the species pool, resulting in a
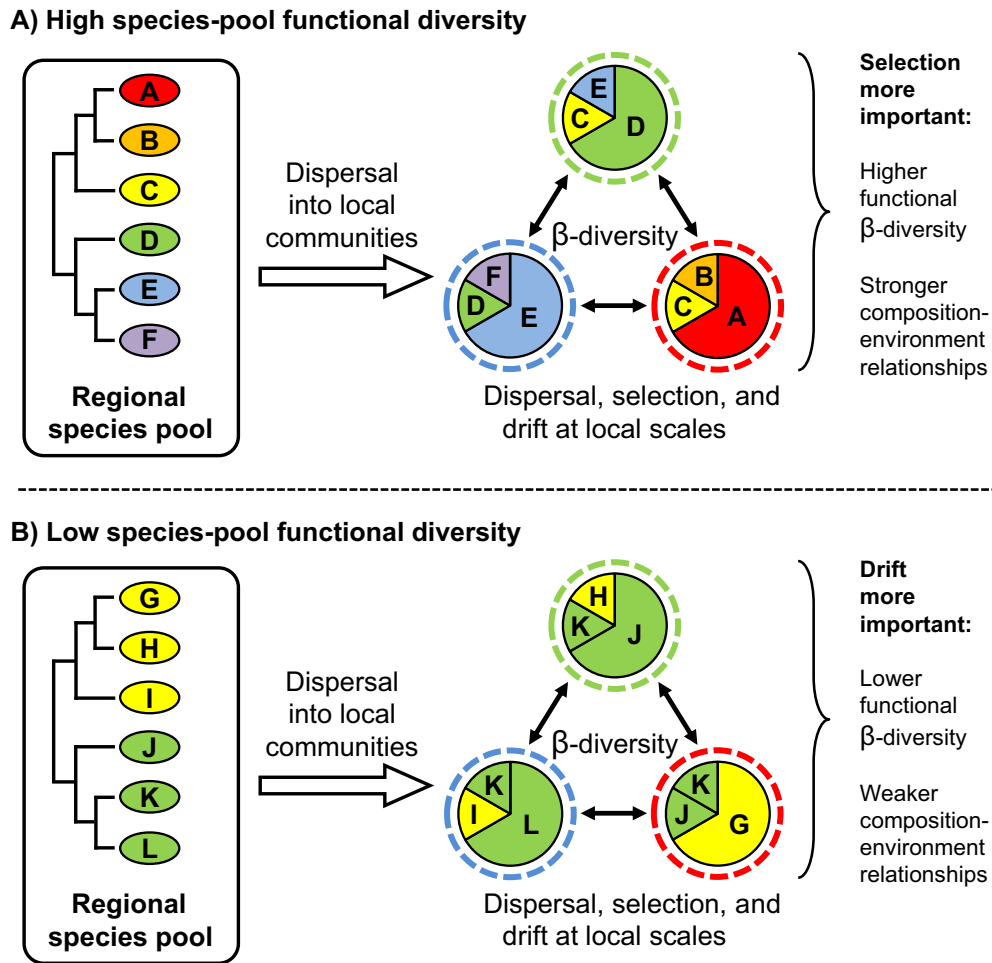
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FIG. 2. A conceptual framework that links species-pool functional diversity (SPFD), fundamental processes of community assembly, and patterns of biodiversity across spatial scales. Models of community assembly typically focus on the importance of species-pool taxonomic diversity in structuring local communities. However, variation in SPFD among regions may mediate the relative importance of niche selection and ecological drift. In this example, two regions (A and B) have identical species-pool richness (six species represented by letters), phylogenetic relatedness, rates of dispersal (arrows) into local communities (circles), and variation in environmental conditions among local communities (dashed colored rings around circles), but differ in the diversity of a trait in the regional species pool (colored ovals). In each local community, environmental conditions select for a particular trait (color of the dashed ring around a local community) and influence the relative abundances of species and trait values (sizes of pie slices); niche selection favors individuals with the red trait in the lower-right community in both regions. In the region with high SPFD (A), niche selection leads to higher variation in trait composition among local communities (functional β-diversity), resulting in strong composition-environment relationships in the region. In the region with low SPFD (B), certain traits are absent from the regional pool, resulting in a relatively stronger influence of ecological drift. This leads to low functional β-diversity and weak composition–environment relationships. This framework can also be extended to understand shifts in assembly processes and patterns of biodiversity within regions over time. For example, SPFD could decrease within a region over time (Fig. 1A vs. 1B) due to biotic homogenization, resulting in a temporal shift in the relative importance of niche selection and ecological drift. Thus, changes in SPFD and its influence on community assembly processes may contribute to differences in biodiversity across regions and changes in biodiversity within region through time.

relatively weaker influence of niche selection and a stronger influence of dispersal history or ecological drift (Fig. 2B). This prediction is based on coexistence theory where functional redundancy in the species pool may reduce fitness differences among co-occurring species (Chesson 2000, Adler et al. 2007) and make the outcome of interspecific interactions more unpredictable (Vellend 2016). Moreover, these conditions increase opportunities for dispersal history or stochastic local extinction to give rise to ecological drift (Hubbell 2001, Vellend 2016). For example, low SPFD may increase the importance of dispersal history (priority effects; Fukami 2015), where variation in the arrival order of species

can increase variation in community composition among sites with similar environmental conditions (Chase 2003). In an experimental study of priority effects in nectar yeast communities, Peay et al. (2012) found that the strength of priority effects between species pairs increased with their phylogenetic relatedness, potentially due to greater functional similarity in nectar resource use and stronger interspecific competition between closely related species. Thus, lower SPFD should generally decrease variation in trait composition among local communities (i.e., functional β-diversity) and weaken relationships between community composition and the environment (Fig. 2B).

These simplified scenarios highlight predictions for how SPFD can influence the relative importance of local niche selection, dispersal, and ecological drift among regions. However, this framework can also be applied to a single region where SPFD changes over time. For example, Devictor et al. (2008) found that changes in land use and landscape fragmentation resulted in the functional homogenization of birds across France, suggesting that biotic homogenization may decrease SPFD over time within a region (a change from Fig. 2A to Fig. 2B). In other cases, SPFD may increase over time (a change from Fig. 2B to Fig. 2A). For example, the relaxation of environmental stressors in alpine tundra has led to upslope movement of non-tundra plant species (Gottfried et al. 2012, Pauli et al. 2012) and an increase in functional diversity (Spasojevic et al. 2013), potentially leading to an increase in SPFD. In summary, our framework focused on differences in SPFD among regions or differences in SPFD within regions over time, has the potential to advance our understanding of how local- and regional-scale processes jointly influence patterns of biodiversity. Below we outline ways to test these hypotheses in studies of community assembly.

TESTING THE INFLUENCE OF SPECIES-POOL FUNCTIONAL DIVERSITY ON COMMUNITY ASSEMBLY

Both observational and experimental studies can provide important insights into how SPFD influences community assembly and both approaches have strengths and weaknesses. Comparisons among sites with different species pools can provide important insights into how SPFD may influence community assembly (Lessard et al. 2012a) and provide a more realistic understanding of how ecological and evolutionary processes operating over long time scales influence local community assembly. However, these types of observational studies will also be confounded by variation in other regional factors such as environmental heterogeneity, land-use history, geographic distances among local communities, and the phylogenetic and taxonomic diversity of the regional species pool (Kraft et al. 2011, Myers et al. 2013). On the other hand, experimental investigations that manipulate SPFD can be used to isolate the effects of SPFD on biodiversity and mechanisms of community assembly (Questad and Foster 2008). However, these approaches are limited in that experimentally constructed species pools do not represent the dynamics that have played out over evolutionary time scales to create the species pools we observe in nature. A combination of observational and experimental approaches will be needed to fully understand the influence of SPFD on biodiversity and community assembly.

Quantifying species-pool functional diversity

A necessary first step in both observational and experimental studies is to quantify SPFD. The regional species pool for a locality can be defined based on several factors including dispersal abilities, biological requirements, and geographic ranges of species in the region (Lessard et al. 2012a, Cornell and Harrison 2014). In addition, the regional species pool can include species absent from a locality that could potentially colonize and establish in it ("dark

diversity"; Partel et al. 2011). In this case, trait data for absent species may be obtained from additional field sampling, herbarium and museum collections, existing trait databases, or by estimating trait values based on the phylogenetic relatedness among absent species and species for which trait data are available (Safi et al. 2011, Lamanna et al. 2014). The most relevant functional traits for a given study will depend on the specific questions asked; therefore, we do not provide recommendations on which functional traits to measure. Instead we reiterate the critical importance of choosing the functional traits most relevant to fitness outcomes under the abiotic and biotic conditions of interest within a given study (Spasojevic and Suding 2012). For example, comparing the influence of SPFD between a water-limited system and a nitrogen-limited system would necessitate measuring functional traits related to both water and nitrogen use. Once the appropriate traits have been measured, SPFD can be calculated using a wide variety of metrics (Schleuter et al. 2010, Mason et al. 2013). Functional dispersion (FDis, which describes dissimilarity in functional traits among species) is a useful starting point because it is independent of species richness and allows for both categorical and continuous traits (Laliberte and Legendre 2010), but the metric(s) used should conceptually match the hypothesis at hand.

To isolate the effects of SPFD in an experimental setting, experimental species pools can be created with varying degrees of functional diversity (Questad and Foster 2008). Experimental species pools may not necessarily be the same as regional species pools, but can be defined as species within a region that can both disperse to and potentially persist in a focal locality ("filtered pools"; de Bello et al. 2012, Cornell and Harrison 2014). Experimental manipulations of filtered pools may be especially useful in species-rich regions or for large organisms in which logistical constraints prevent the collection or manipulation of large numbers of species or individuals. To directly test the influence of SPFD alone, other factors that may vary among regions in observational studies need to be controlled for, including: species-pool richness (e.g., γ-diversity), mean values for functional traits, and phylogenetic diversity (Fig. 3). Without controlling for these other factors, it will not be possible to test how SPFD influences community assembly independently of variation in species-pool richness or variation in phylogenetic diversity. Maintaining similar mean trait values is important so that influences of trait diversity are tested and not differences in mean trait values that often correlate with differences in life-history strategies related to growth, survival, or defense. For example, differences in mean body size among species pools would reflect a shift in growth rate among organisms (e.g., a shift from faster to slower), while a shift in the diversity of body size among species pools would reflect a shift variation in growth rate among pools (e.g., low variation in growth rate to high variation in growth rate with the same mean). Maintaining similar phylogenetic diversity while varying trait diversity among experimental pools may be especially difficult if traits are highly conserved (Wiens et al. 2010), but is important if the goal of the study is to test the influence of functional diversity independent of phylogenetic diversity (Safi et al. 2011). To aid researchers in this endeavor, we include an empirical
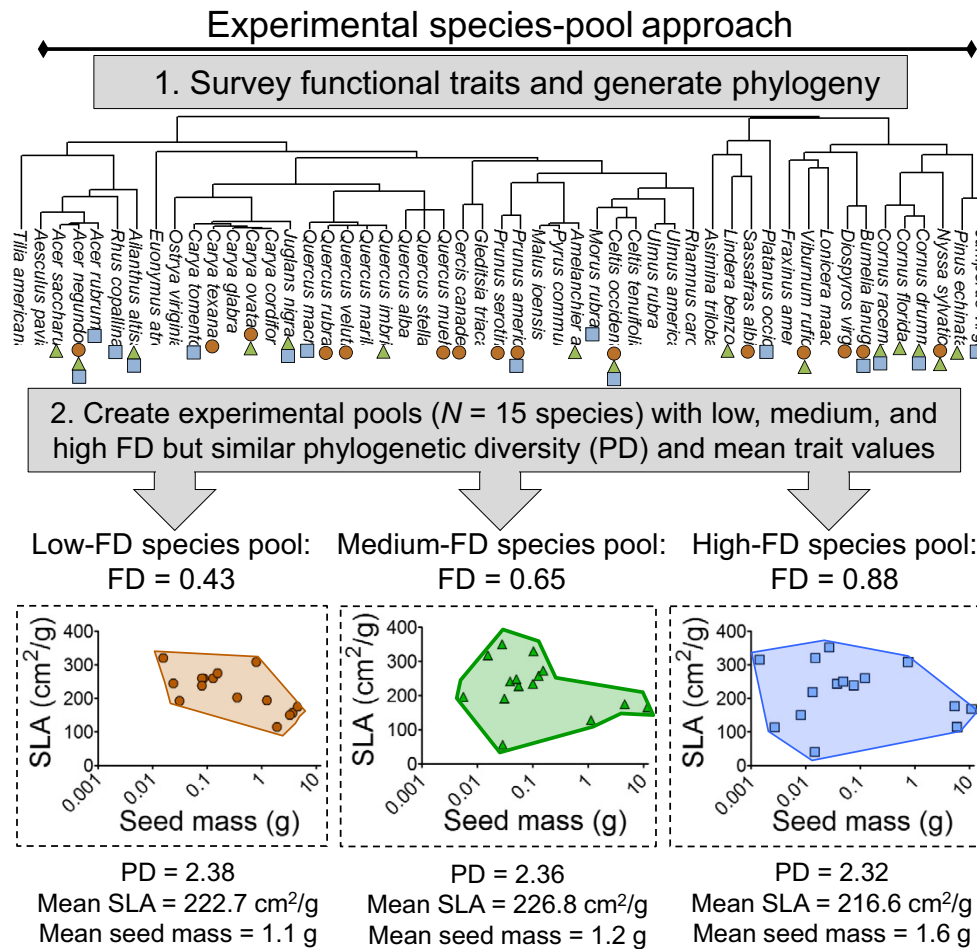
Fig. 3.   Overview of an experimental approach for manipulating species-pool functional diversity. In this example, we used a molecular phylogeny (based on rbcL, matK, and trnL-trnF created using phyloGenerator [Pearse and Purvis 2013]) and trait data for specific leaf area (SLA) and seed mass for 50 Ozark tree species (species names intentionally truncated; Spasojevic et al. 2014*b*) to create experimental species pools with low (brown), medium (green), or high (blue) functional diversity (FD). Species selected for each pool are indicated by colored shapes at the tips of the phylogeny. Species-pool functional diversity (dashed boxes) with low, medium, and high functional diversity is illustrated using convex hulls around trait data; FD was calculated using functional dispersion (FDis). Each pool has equal species richness (N = 15), similar phylogenetic diversity (PD; summed branch lengths), and similar mean trait values. The R code used to create these experimental pools is provided in Data S1.

example and overview of this approach in Fig. 3 and R code (Data S1) to create experimental pools that vary in SPFD while maintaining species-pool richness, mean trait values, and phylogenetic diversity. Once experimental pools have been defined, "SPFD" treatments can be employed to test a variety of hypotheses concerning how changes in SPFD influence the relative importance of dispersal, niche selection, and ecological drift on patterns of biodiversity.

Testing the relative importance of community assembly mechanisms

There are potentially many ways to test the influence of SPFD on various community assembly mechanisms. Here we provide examples to illustrate how both macroecological studies based on observational data and small-scale experiments can be used to test the influence of SPFD on niche selection, dispersal, and ecological drift. First, the influence of SPFD on the relative importance of niche selection and

ecological drift can be tested in observational studies by comparing patterns (alpha- or beta-diversity) and mechanisms of biodiversity across regions that differ in SPFD. For example, one could compare patterns of functional β-diversity across soil-resource or topographic gradients in regions that differ in SPFD, use variation-partitioning to determine the amount of variation in β-diversity explained by environmental heterogeneity and spatial variables, and then use null-models to examine the influence of SPFD in the in the absence of local assembly processes. Coordinated research networks such as the Smithsonian Forest Global Earth Observatory (ForestGEO) Network (Anderson-Teixeira et al. 2015), The Nutrient Network (NutNet; Borer et al. 2014), or Long-Term Ecological Research (LTER) sites may be particularly useful for examining this question for plants. The specific analytical approach will ultimately depend on the particular question at hand, but we generally recommend that such observational studies use multiple analytical approaches to tease out how SPFD influences community

assembly including null-model analyses of spatial or temporal variation in community composition, species–environment or trait-environment relationships, variance partitioning of spatial and environmental factors, and/or analyses of trait over-/under-dispersion in local communities (Legendre et al. 2005, Brown et al. 2014, Swenson 2014, Mori et al. 2015, Ovaskainen et al. 2017).

Second, the influence of SPFD on the relative importance of niche selection and ecological drift can be tested by creating experimental pools that differ in SPFD (Fig. 3) and assembling communities from these pools (e.g., adding seeds, creating micro/mesocosms). For example, a low, medium, and high SPFD seed mix (Fig. 3) could be added to plots that differ in environmental conditions to assess how SPFD may influence species sorting along environmental gradients. This approach, while less realistic than a macroecological approach, allows for a clearer understanding of the direct influence of SPFD as it allows for greater control of variation in species-pool richness, mean values for functional traits, and phylogenetic diversity, which all vary along macroecological gradients. Such experimental approaches can also allow for examinations of how SPFD influences the relative importance of different assembly mechanisms. For example, the influence of SPFD on ecological drift could be tested by experimentally manipulating both SPFD and the number of individuals in local communities in a factorial design, where ecological drift is expected to have a stronger influence in smaller communities with fewer individuals (Hubbell 2001). This could be achieved by creating experimental pools that differ in SPFD and then factorially assembling communities in mesocosms from those pools that differ in the number of individuals added to local communities. Moreover, the influence of SPFD on the relative importance of dispersal history (e.g., priority effects) could be assessed using the same approach outlined in Fig. 3, but with additional treatments that manipulate the arrival order of species from experimental pools that differ in SPFD (e.g., functional similarity of traits related to resource competition; Peay et al. 2012).

IMPLICATIONS OF SPECIES-POOL FUNCTIONAL DIVERSITY FOR CONSERVATION AND RESTORATION IN CHANGING ENVIRONMENTS

Unprecedented levels of anthropogenic environmental change require management practices that restore degraded ecosystems and conserve biodiversity and ecosystem functions. Such practices include species reintroductions, reestablishment of disturbance regimes, control and prevention of invasive species, and actions that increase resistance and resilience to global change. Consideration of spatial or temporal changes in SPFD may improve predictions for restoration outcomes and conservation efforts focused on ecosystem resistance/resilience to environmental change.

Species-pool functional diversity and ecosystem restoration

Recently, Brudvig et al. (2017) highlighted the need for resolving unpredictability in restoration outcomes, stating that much variation arises from restoration context: how, where, and when restoration is conducted. For example,

disturbance (e.g., fire, logging, grazing) and species reintroductions are often used to restore ecosystems to contain characteristic assemblages of the species that occur in reference ecosystems (Society for Ecological Restoration International Science & Policy Working Group 2004). Yet similar disturbance treatments often have variable and unpredictable effects on biodiversity (Catano et al. 2017). While factors such as land-use history and environmental conditions are important contextual considerations for understanding restoration outcomes (Hobbs and Harris 2001, Suding 2011), the properties of the regional species pool, particularly SPFD, may be an important determinant of restoration outcomes (Zobel et al. 1998, Brudvig and Mabry 2008). Grman and Brudvig (2014) found that restoration outcomes *within* restored prairies were unrelated to the species-pool richness used in seed mixes, suggesting that species-pool richness alone may not be a good predictor of restoration outcomes. Interestingly, across 18 disturbance experiments, Myers and Harms (2009b) found that the effect of seed additions on local species richness was unrelated to the number of species in experimental species pools, but positively related to the functional diversity of those pools (variation in seed size). Furthermore, land managers often seek to restore or manage β-diversity in an effort to mitigate biotic homogenization and maintain diversity at landscape scales. For instance, in a meta-analysis, Catano et al. (2017) found plant β-diversity declined most following disturbance when experimental species pools had more species; however, Questad and Foster (2008) showed that β-diversity in grasslands can increase following disturbance when the experimental pool contains diverse plant functional groups. Together these studies suggest that SPFD may be an important context for understanding the efficacy of practices that seek to restore ecosystems degraded by human activities. Although most empirical examples tend to come from plant communities, our SPFD framework can equally apply to restoration practices focused on animal or microbial species (e.g., wildlife reintroductions, restoring fungal symbionts).

Species-pool functional diversity and ecosystem resistance and resilience

Rapid and unprecedented environmental change requires conservation practitioners to increase the resistance and resilience of ecosystems to biological invasions and novel environmental conditions (Elmqvist et al. 2003, Angeler and Allen 2016). Importantly, functional diversity may increase resistance and resilience within a given ecosystem via two mechanisms. First, in regions with low SPFD, the function of any given species lost to environmental change can be replaced by other functionally redundant species in the ecosystem (Holling 1973, Elmqvist et al. 2003). For example, after the loss of herbivorous fish, Jamaican coral reefs were able to remain a coral-dominated system due to compensation by herbivorous sea-urchins. However, once a pathogen reduced urchin populations, the ecosystem lost resilience and shifted to an algae-dominated system (Nystrom et al. 2000). Similarly, SPFD may influence the resistance of entire regional biotas to species invasions or environmental change. For example, the outcome of species invasions on local communities can depend on the

functional similarity of native and invasive species (Funk et al. 2008, Laughlin 2014). High SPFD could increase species invasions if it decreases functional redundancy among native and exotic species. However, high SPFD could potentially decrease species invasions if it increases the probability that the species pool contains native species that may outcompete or preempt exotic species. Second, in regions with high SPFD, functional diversity can increase resistance and resilience when regions that contain a diverse set of response traits are buffered against environmental change (Holling 1973, Elmqvist et al. 2003). For example, restoration practices that maintain high SPFD may increase ecosystem resilience in productivity to wildfire by maximizing the diversity of fire-tolerant traits (Spasojevic et al. 2016). Considering spatial and temporal changes in SPFD may offer novel biological predictions and management options to guide community reassembly and to create adaptive ecosystems that are resilient and resistant to unpredictable futures.

Conclusions and Future Directions

Despite decades of research on the species-pool concept and the recent explosion of interest in trait-based frameworks in ecology, restoration, and biogeography, surprisingly little is known about how spatial and temporal changes in SPFD influence the fundamental processes of community assembly. By integrating dynamic regional species pools into trait-based assembly frameworks, ecologists will be better poised to resolve many long-standing questions regarding the causes and consequences of biodiversity. In particular, changes in SPFD across biogeographic regions and temporal changes in SPFD within regions represent a critical, yet understudied, factor influencing the relative importance of niche selection, ecological drift, and dispersal in community assembly. We conclude with four key questions for future research on the causes and consequences of SPFD:

1) How do relationships between SPFD and species-pool richness change across organisms and scales? The relative influence of different components of species-pool diversity (e.g., functional, taxonomic, phylogenetic) on patterns and processes in ecological communities will depend on the nature of the relationships among them (Fig. 1). However, comparative studies and syntheses of these relationships are lacking (Safi et al. 2011, Lamanna et al. 2014, Swenson et al. 2016).

2) To what extent do spatial and temporal changes in SPFD reflect the influence of regional-scale and local-scale processes? Species-pool frameworks often depict community assembly as a top-down process from the regional species pool to local communities (Fig. 2). However, processes at local scales can feedback in a bottom-up way to influence the regional species pool (Mittelbach and Schemske 2015). Understanding when and where SPFD is determined by processes at different scales is central to the integration of biogeography, ecology, and global-change biology.

3) How does the relative importance of different processes that influence SPFD vary systematically along broad-scale gradients in climate or productivity? Several hypotheses exist to explain large-scale gradients of species diversity (e.g., greater speciation rates in the tropics, stable environmental conditions). Do these also apply to SPFD, and if so how?

4) To what extent can changes in SPFD predict whether environmental change homogenizes or diversifies community composition? In some cases, strong selection for species with disturbance-tolerant traits leads to the homogenization of communities while, in other cases, disturbance results in species sorting across environmental gradients. The extent to which these contingent responses to disturbance are explained by the influence of SPFD on local assembly mechanisms is unknown.

Future studies that address these four questions will advance our understanding of the joint importance of both regional-scale and local-scale processes in influencing patterns of biodiversity within and among communities and will have important implications for linking the regional species-pool concept and trait-based assembly theory with conservation, restoration, and global change.

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Supporting Information

Concepts & Synthesis