CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Community assembly and the functioning of ecosystems: how metacommunity processes alter ecosystems attributes

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Abstract. Recent work linking community structure and ecosystem function has primarily focused on the effects of local species richness but has neglected the dispersal-dependent processes of community assembly that are ultimately involved in determining community structure and its relation to ecosystems. Here we combine simple consumer-resource competition models and metacommunity theory with discussion of case studies to outline how spatial processes within metacommunities can alter community assembly and modify expectations about how species diversity and composition influence ecosystem attributes at local scales. We argue that when community assembly is strongly limited by dispersal, this can constrain ecosystem functioning by reducing positive selection effects (reducing the probability of the most productive species becoming dominant) even though it may often also enhance complementarity (favoring combinations of species that enhance production even though they may not individually be most productive). Conversely, excess dispersal with strong source-sink relations among heterogeneous habitats can reduce ecosystem functioning by swamping local filters that would normally favor better-suited species. Ecosystem function is thus most likely maximized at intermediate levels of dispersal where both of these effects are minimized. In this scenario, we find that the selection effect is maximized, while complementarity is often reduced and local diversity may often be relatively low. Our synthesis emphasizes that it is the entire set of community assembly processes that affect the functioning of ecosystems, not just the part that determines local species richness.

Key words: dispersal limitation; ecosystem function; local diversity; metacommunity; R*; regional diversity; species sorting.

INTRODUCTION

More than 20 yr of research has decisively shown that communities with higher local species richness typically have higher levels of ecosystem functioning (e.g., Cardinale et al. 2012, Tilman et al. 2014), which implies that conserving biodiversity can help protect the "health" of natural ecosystems, and provide ecosystem services to humans (e.g., Hooper et al. 2012). There are two main drivers that determine the Biodiversity-Ecosystem Function (BEF) relationship. First, selection effects occur when a more diverse species pool is more likely to contain and favor those species that most contribute to ecosystem functioning than a smaller species pool. Positive selection effects have been commonly reported for biomass-focused BEF studies, but negative selection effects in which competitively dominant species contribute less to ecosystem function than other species have also been reported, especially for other ecosystem functions (Jiang et al. 2008). For simplicity, we ignore these more complicated selection effects. Second, complementarity occurs when the presence of more species can enhance ecosystem functioning if species occupy distinct niches at the local scale (Loreau and Hector 2001, Fox 2005). Like selection effects, complementarity has also been wide documented in BEF studies as contributing to higher ecosystem functioning in more diverse communities (e.g., Loreau and Hector 2001).

Although both selection and complementarity are important in determining BEF relationships, these

processes are also influenced by the numbers and types of species present in any given local community. Ultimately, it is the entire set of community assembly processes that determines local species diversity and composition (including the trait distributions of organisms), and it is the result of these processes that then determines how selection effects and complementarity emerge. The link between selection effects and complementarity effects and community assembly is sometimes overlooked because, by necessity, BEF studies are typically conducted in small experimental plots or microcosms that ignore the larger spatial context of community assembly (but see Fukami et al. 2010). Thus our understanding of BEF relationships is strongly biased on the local scale, where we expect species interactions to occur, with little attention to how the broader spatial context influences community assembly and the resulting BEF relationships. Since local communities rarely assemble independently from larger-scale processes, it is critical to study the interplay between regional and local processes (Bond and Chase 2002, Loreau et al. 2003, Mouquet and Loreau 2003, Gonzalez et al. 2009, Shanafelt et al. 2015, Thompson and Gonzalez 2016).

The local-scale focus of BEF relationships (Fig. 1a), unfortunately, creates a conundrum for those wanting to justify conservation policies via the positive effect of biodiversity on ecosystems. Some recent meta-analyses have shown that at small scales local biodiversity is often not declining and may even sometimes be increasing (Vellend et al. 2013, Dornelas et al. 2014, Elahi et al. 2015); even in the face of experimental perturbations (Supp and Ernest 2014). This has led some to question the relevance of BEF studies (Srivastava and Vellend 2005, Vellend et al. 2013). While these results have been questioned or contradicted (Murphy and Romanuk 2014, Wright et al. 2014, Newbold et al. 2015, Gonzalez et al. 2016), it is

clear that local diversity is not always, or maybe even often, declining through time even in the face of an apparent ongoing mass extinction at the global scale (Ceballos et al. 2015).

A simple way to think about larger scale effects on local diversity (Fig. 1b) is to invoke a commonly found strong correlation between regional and local biodiversity (Cornell and Lawton 1992, Shurin et al. 2000). If this were true, maintaining high regional biodiversity would then ensure high local diversity; protecting regional biodiversity would therefore be important for maintaining local ecosystem function. However, which species coexist and at which scale, how well suited their traits are for the local environment, and how those traits complement those of other species are all potentially important factors influencing ecosystem function (Fig. 1c). These factors emerge from community assembly processes but are not necessarily tightly related to the number of species that coexist at the local scale. Instead, patterns of diversity and composition depend on dispersal and connectivity among communities, as well as environmental heterogeneity and disturbance rates in the region. Integration of these aspects of community assembly have largely been missing from BEF studies (but see Ptacnik et al. 2010, Thompson and Gonzalez 2016).

So how do community assembly processes influence BEF relationships and how should we go about integrating regional and local biodiversity? Community assembly is influenced by a number of processes (competition, predator-prey relations, priority effects, historical contingency, etc.) and many different models could be used to illustrate how spatial processes influence how community assembly and species traits impact ecosystem function. For simplicity, we focus on basic resource competition theory (e.g., Tilman 1982) within the context of metacommunities to illustrate the important role of
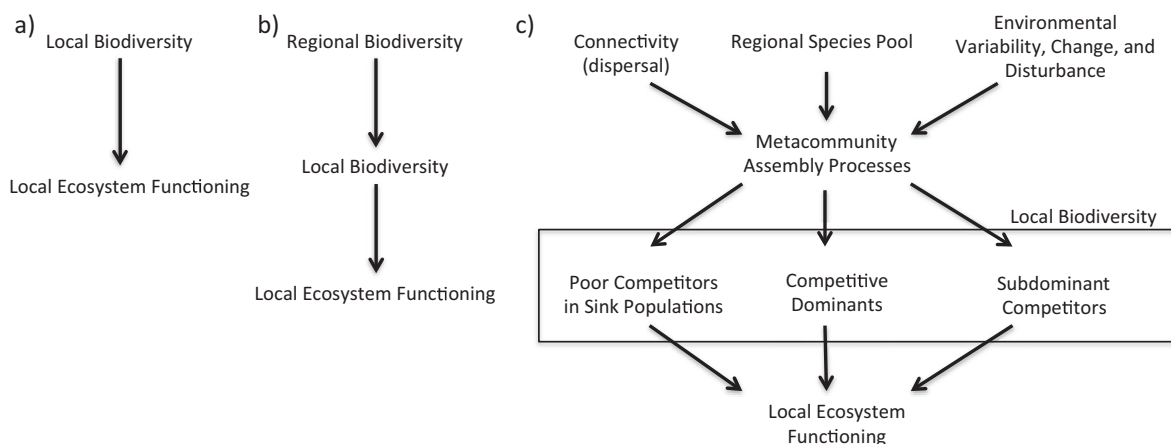

FIG. 1. Three increasingly complex conceptual views of how biodiversity affects ecosystem functioning: (a) a direct causal relation between local biodiversity and ecosystem functioning, but the effects of the regional species pool are ignored. (b) Regional biodiversity as an ultimate driver of local biodiversity but with the assumption that this relationship is simple (e.g., monotonic). (c) The metacommunity view in which multiple drivers (connectivity and environmental variability and change, as well as regional biodiversity) affect different components of local diversity (poor competitors that exist as sink populations, subdominant species, and competitively dominant species) that then differentially affect ecosystem functioning.

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community assembly on ecosystems, while recognizing that a more comprehensive approach, especially involving other types of species interactions, will be needed in the future.

We identify three qualitatively distinct metacommunity scenarios, each of which favors species with distinct traits and thus roles in BEF relationships. The first is "dispersal sufficiency", when dispersal is sufficient to overcome dispersal limitation, but not substantial enough to support important source-sink relations among patches. Here, local communities should be composed of species that are best suited to the local sites, which we refer to as "competitively dominant" species. The second is dispersal surplus, when emigration of competitive dominants and immigration of less competitive species create source-sink relations among patches. Immigration supports species less suited to the local conditions, which we refer to as "poorly competitive" species, and these species reduce ecosystem function by reducing the relative abundance of competitive dominants even though species richness may be enhanced. It also does not enhance complementarity. Thirdly, dispersal limitation, where some competitive dominants are missing from some local ecosystems due to limited colonization or extinction. In these cases, species which we refer to as "subdominant" (e.g., transient, weedy) may thrive in a given locality, but contribute less to overall ecosystem functioning because they possess traits suited to alternate habitats or ecological strategies. We argue that the relative importance of dispersal and the prevalence of these three types of species varies depending on the metacommunity context including disturbance, habitat connectivity/isolation, environmental context and change, and the nature of the species pool, and that this in turn moderates BEF relationships (Fig. 1c).

DISPERSAL SUFFICIENCY: THE CASE OF SPECIES SORTING AND ECOSYSTEM FUNCTION

We start with the idealized "species sorting" case (sensu Leibold et al. 2004, Holyoak et al. 2005). Here, species from a regional pool sort among localities according to how well they perform and compete in different environmental conditions (Tilman 1982, Chase and Leibold 2003). Meta-analyses suggest that many metacommunities show strong relationships between species compositional variation and environmental variation (Cottenie 2005, Soininen 2014), indicating that the species-sorting framework is a reasonable foundation on which to start.

In Box 1, we use resource competition theory (e.g., Tilman 1982) to illustrate the intersection between resource competition and metacommunity theory and highlight how species sorting can influence ecosystem function. We assume each patch is internally homogeneous. If relative resource use by a community (as indicated by ΔR_{opt} in Box 1) is correlated with ecosystem function (e. g., Tilman et al. 1997, Gross and Cardinale

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Box 1. Community assembly and the functioning of ecosystems under dispersal sufficiency

Following Tilman et al. (1997) and its elaboration by Gross and Cardinale (2007), we use the graphical representation of consumer-resource dynamics with zero-net-growth isoclines (ZNGIs) and impact vectors (which include both consumption and possible recycling (Daufresne and Hedin 2005), to illustrate resource competition for two essential abiotic resources across a gradient in relative supply. We assume minimum possible requirements for one resource are negatively constrained by the other resource (R_{opt}, bold dashed lines in Fig. 2a) and all species have the "corner" (i.e., the point of colimitation by both resources) of their ZNGIs on this function. ΔR_{opt} compares how well a given species or pair of coexisting species (with resource requirements equal to R_i^* for both resources) suppress resource levels compared to levels expected if the resident species were the absolute best idealized competitor in that ecosystem whose ZNGI included the corresponding value of R_{opt}.

When two species compete for two resources (Fig. 2a, b), intermediate resource ratios favor coexistence and ecosystem function is higher when both species are present due to complementarity. When the supply of resource-ratios are skewed towards one resource, the species that can use the less abundant resource more efficiently outcompetes the other and ecosystem function is maximized by only one species as a result of selection effects.

When there are three species present in the pool, there is enhanced functioning along a range of relative supply rates (Fig. 2c, d). If one of the species goes regionally extinct, then the remaining species expand their habitat distributions. This allows them to coexist by resource partitioning and thus show enhanced complementarity. As a result, local diversity remains unchanged (either one or two species, depending on resource ratios) even though regional diversity declines by 33%. Despite constant local diversity, average ecosystem function across the metacommunity declines due to the extinction. In this scenario however, the selection effect is stronger than the complementarity effects (comparing ecosystem function in the presence of the intermediate species that contributes to selection over intermediate resource supply rates with the complementarity between the other two species in its absences).
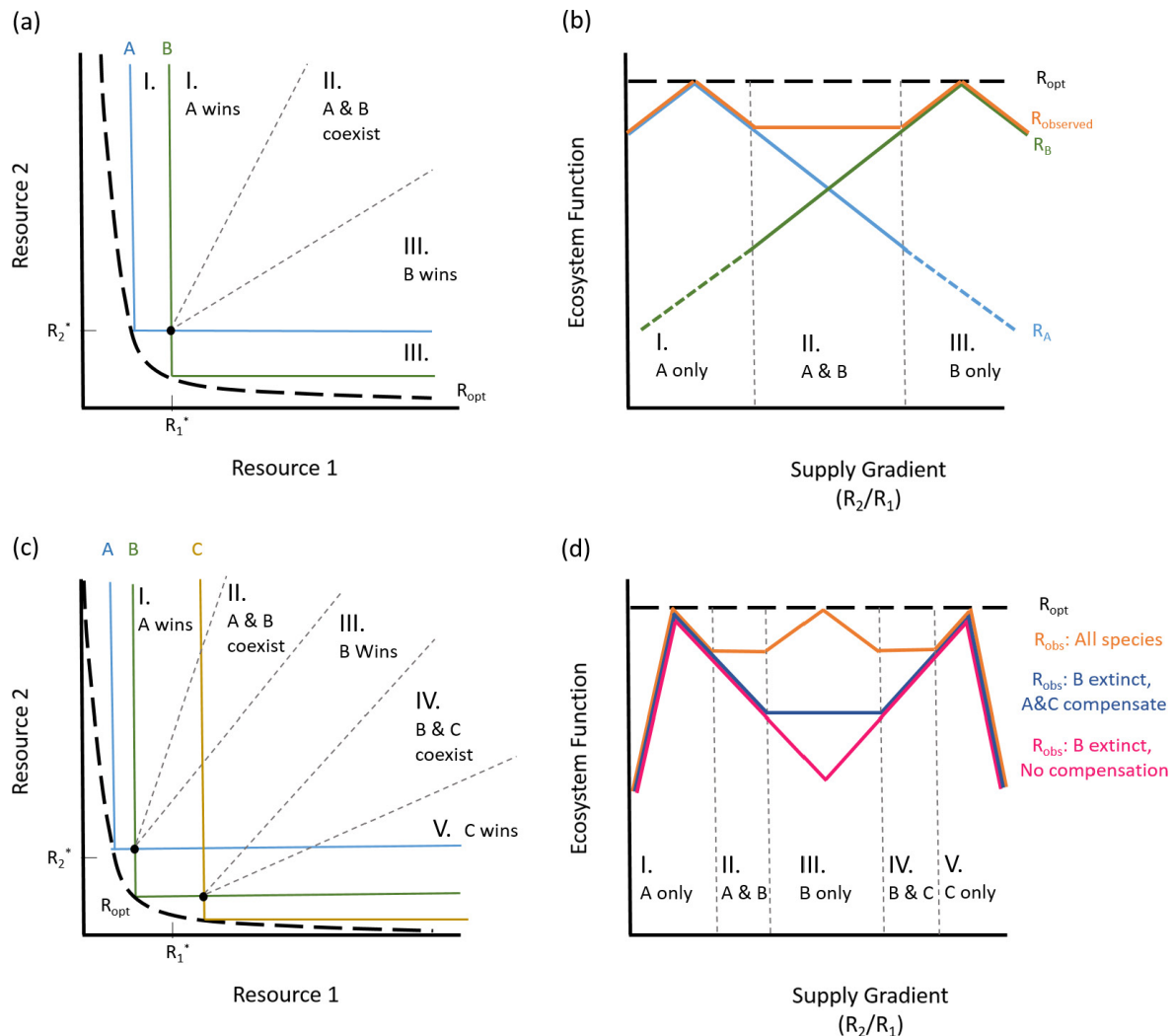
Fig. 2. (a) Competition between two species (A and B) for two essential resources (R_1 and R_2). Solid elbow-shaped lines are the Zero Net Growth Isoclines (ZNGIs) for each species; the vertical component is the minimum requirement for population growth limited by resource 1, the horizontal component is that on resource 2. The two species coexist at steady state (zero growth for both species) only at one set of resource concentrations (solid point where $R_i = R_i^*$) where each species is limited by a different resource. Coexistence depends on how well resource supply (resource concentration in the absence of any consumption) corresponds to the relative uptake rates by the two species (fine dashed lines, which also define region of possible coexistence). R_{opt} (heavy dashed curve) denotes expected R_1^* and R_2^* levels if species were theoretically available that could perfectly use the available resources along a gradient of R_1 and R_2 values (b) Effects of species composition on ecosystem function. Ecosystem function ($R_{observed}$) differs with varying nutrient supply ratios (R_2/R_1) if both species are present in the regional species pool (solid orange line) or if only species one species is present (blue or green lines). Dashed blue or green lines show expected ecosystem function contribution of the competitively excluded species, if the dominant species were not present. Panels (c) and (d). Effects of extinction on species sorting in a three species metacommunity in a scenario. (c) ZNGI's, competitive exclusion and coexistence spaces for species A, B, and C. Black dots denote stable coexistence points. (d) Ecosystem function in habitats along a supply gradient. Orange: when all species are present in regional pool and can sort into local communities. This shows maximal ecosystem function across this gradient with these three species in the pool. Blue: when species B goes regionally extinct and A and C replace B where they can. Ecosystem function in region IV is lower than with all species because A and C do not use resources in this supply range as efficiently (see panel a). Pink: when species B goes extinct, but A and C do not colonize communities formerly dominated by B. A similar pattern can happen if B is in the metacommunity but dispersal limitation prevents it from reaching suitable habitats.

2007), the match between the environment and species' traits is critical to maximize resource use. Species with a diversity of traits in the regional species pool improves the probability that species that maximize ecosystem function can colonize any given patch. In Box 1, only one species is necessary to maximize function when resource ratios are highly skewed. However, if a metacommunity contains habitat types that vary in resource supply, then the identity of the species that maximizes ecosystem function will vary for each habitat. It is the species sorting

process at the metacommunity scale that allows the species (and species combinations) that are most effective in a given environment to occur across the different habitat types. If a landscape contains heterogeneous habitats representing a variety of resource supply ratios, a metacommunity containing only one species would have lower average functioning across this entire region than if multiple species were present and able to optimally sort themselves along environmental gradients. It is therefore diversity at the metacommunity scale, and the ability of the species sorting process to select for species whose traits allow them to most effectively function in a given habitat, that is critical for ecosystem functioning.

If the species best suited to the local conditions is missing, multiple coexisting species can result in higher ecosystem function than a single species alone (Box 1). Under these conditions, niche differences among species (i.e., complementarity) may allow several coexisting species to maintain ecosystem function closer to the theoretical optimum than any single species would. Niche complementarity often occurs at very small scales (e.g., variation in rooting depth in plants, diet partitioning in animals) which can influence BEF. However, the frequent observation of a positive local BEF relationship (e.g., Cardinale et al. 2012, Hooper et al. 2012) may also suggest that species composition in many localities is constrained away from optimal trait values because of the constraints of the regional species pool or because of other metacommunity processes such as "dispersal-limited" metacommunity assembly (*Dispersal limitation: the case with colonization-extinction patch dynamics*).

A key prediction emerges from a species-sorting view of BEF relationships; under imperfect species sorting, there may be a negative relationship between selection effects and complementarity. If selection effects are strong enough (i.e., an extremely well suited species for that environment exists in the species pool), it should lead to decreased local diversity and decreased complementarity. The role of the selection effect will depend on the species pool and the distribution of ecological traits it encompasses.

An analysis of the Jena Experiment (Rychtecká et al. 2014; Fig. 3), a long-running biodiversity experiment in Germany, provides some support for this prediction. As expected there was an overall positive relationship between the number of species present and ecosystem function across the whole experiment, largely due to the species richness treatments themselves. Within each richness treatment, in contrast, actual species richness was negatively correlated with biomass. This suggests that when selection effects are high (because the best competitor is present in the species pool for a given richness treatment), ecosystem function is high even though local species richness is low; when selection effects are weaker, local species richness is higher (likely involving complementarity) even though ecosystem function is lower. That is, coexistence via complementarity is favored when competitive dominants are absent but function is also lower.
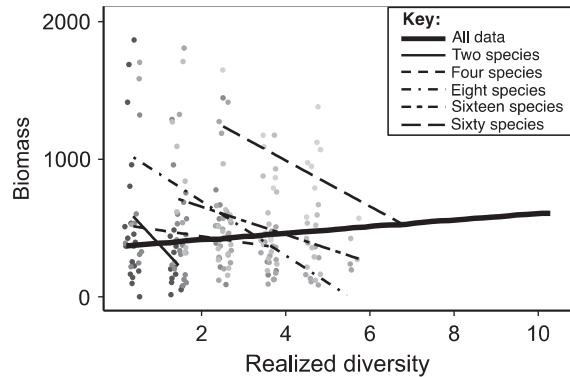

FIG. 3. Analysis of diversity biomass relations in the Jena experiment. The experiment manipulated species pool size (the number of species initially sown into the experiment and maintained by subsequent weeding) by random selection of subsets of different sizes from a maximum pool of 60 species. The data are separated into the various manipulations of species pool size (different line type indicate species pools as shown in the inset and symbols are progressively darker for smaller pool sizes). The ordinate shows the actual number of species remaining in each plot (points have been jittered for clarity) and the abscissa indicates total above-ground biomass as a measure of ecosystem function. Data are re-plotted from Rychtecká et al. (2014). Correlations between biomass and realized diversity are all negative (three out of five are significantly so at 0.05 level) as reported by the original authors. The overall correlation however (bold solid line across all plots) is significantly positive.

In summary, resource competition models suggest that the numbers of species and associated traits in the species pool influence both local community assembly and ecosystem function (see also Grace et al. 2016). This combination of local and metacommunity processes leads to correlations between regional species richness and average local ecosystem functioning but not necessarily between local richness and ecosystem functioning. However, the simple approach we took in this section assumes an intermediate dispersal rate that optimizes species sorting or a "Goldilocks" effect; "not too much and not too little… just right." But the world is rarely "just right."

DISPERSAL SURPLUS: THE CASE OF SOURCE-SINK DYNAMICS

High dispersal rates among patches in the metacommunity can lead to source-sink effects (also known as "mass effects"), where high dispersal rates maintain species where they could not otherwise persist (e.g., Loreau and Mouquet 1999, Amarasekare and Nisbet 2001, Mouquet and Loreau 2003). As a result, source-sink ecosystems may have lower ecosystem function than if dispersal were lower (Bond and Chase 2002, Mouquet et al. 2002, Mouquet and Loreau 2003) even though high dispersal may also elevate local biodiversity. Haegeman and Loreau (2015) illustrate this with a simple model (see also Amarasekare and Nisbet 2001, Mouquet and Loreau 2003, Ryabov and Blasius 2011) that considers competition between habitat generalists that differ in their degree

of habitat specialization under different levels of dispersal. Under very low dispersal, each species is restricted to its preferred habitat where it most strongly reduces local resources. As dispersal increases, emigration to less suitable habitats increases. The ability of species to reduce local resources declines in these less suitable habitats while simultaneously facilitating co-occurrence of species at the local scale. At very high dispersal, coexistence at the meta-community scale becomes increasingly difficult and eventually only one species is present but is less able to suppress resources across all the habitats.

Although source-sink dynamics can disrupt local control of communities and alter ecosystem function, empirical evidence for this effect is limited. While some empirical studies suggest that negative source sink/mass effects on ecosystem function can be created with relatively low dispersal (e.g., ~10% exchange per generation; de Boer et al. 2014), most studies we know of indicate that dispersal rates of 40–100% per generation are needed to trigger compositional and ecosystem impacts (Kunin 1998, Cottenie et al. 2003, Howeth and Leibold 2010, Lindström and Östman 2011). This suggests that reduced ecosystem function from dispersal surplus is unlikely, except under exceptional circumstances (e.g., strong directional flow of organisms across habitat boundaries) or at very small scales where dispersal exchanges are of similar magnitude to the population turnover rates of the organisms involved. An additional constraint on the role of dispersal surplus as it is generally modeled is that it ignores habitat selection behavior (and other adaptively biased forms of dispersal) that likely reduce the consequences for ecosystem functioning.

DISPERSAL LIMITATION: THE CASE WITH COLONIZATION-EXTINCTION PATCH DYNAMICS

Dispersal limitation reduces the propensity for species to find their favored environmental conditions (Mouquet et al. 2002, Ozinga et al. 2005), such that species with the best match to a local environment—and thus most able to maximize ecosystem function—may often be absent (Box 2). Because of this, a metacommunity with low

dispersal or low connectivity among patches may take some time to reach the endpoint community that also maximizes ecosystem function (e.g., after an abrupt environmental change), if it reaches that state at all. Depending on colonization/extinction rates and rates of environmental change/disturbance, many local communities would be at intermediate stages of community assembly and dominated by subdominant species that can persist in a local environment only when the competitively dominant species is absent. These intermediate communities can have similar, or even higher, species richness as the final one, but with lower ecosystem functioning (being further from the R_{opt} line) because these subdominant species do not contribute as strongly to ecosystem function.

To illustrate how species-sorting and dispersal limitation within a metacommunity can influence local-scale ecosystem function, we highlight two studies. The first case study is from a long-term study of a desert rodent assemblage, where a dominant group of species (the kangaroo rats *Dipodomys* spp) were experimentally removed from large fenced plots (Ernest and Brown 2001, Thibault et al. 2010). In plots where kangaroo rats were removed, the species richness of rodents initially rebounded to nearly control levels but total rodent energy use (a measure of ecosystem functioning) was substantially less than in plots with kangaroo rats (approximately 14% of controls, Ernest and Brown 2001; Fig. 5). Eighteen years later, a new species, *Chaetodipus baileyi*, colonized the experimental plots, decreasing richness but increasing energy use to nearly 80% of the values on the control plots. This species had occurred in the broader metacommunity for decades, but some limitation on its dispersal seems to have delayed the species' presence in the experimental plots.

A second case study comes from the Jena grassland BEF experiment (Petermann et al. 2010). The authors showed that the traditionally observed positive BEF relationship held in communities that were closed to immigration (i.e., unwanted immigrants were deliberately removed; Fig. 6). However, in subplots in which species from the regional pool were allowed to reinvade on their own (spontaneous invasion), or assisted through seed

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Box 2. Community assembly and the functioning of ecosystems under dispersal limitation

We use the simple resource competition model we discussed in Box 1, but with a more diverse species pool (Fig. 4). The endpoint community that emerges in a given locality depends on local environmental conditions (e.g., supply ratio of resources) and consists of either single species with ZNGIs that are closest to the physiological constraint line (R_{opt}) for that supply ratio, or by pairs of coexisting species. Community configurations consisting of the best species (shown with solid symbols in Fig. 4) for that resource supply ratio are stable and resistant to invasion, but they can only exist if those particular species can actually reach that location. Until those best-suited species colonize, other species with ZNGIs that are more distant from R_{opt} can inhabit this resource-state space (with consequent resource levels shown in open symbols in Fig. 4; Leibold 1998). We call these species "subdominant"; species that are sufficiently well-suited to a given supply ratio to persist in a given locality, but can be outcompeted by other species better suited to those conditions when/if they arrive.
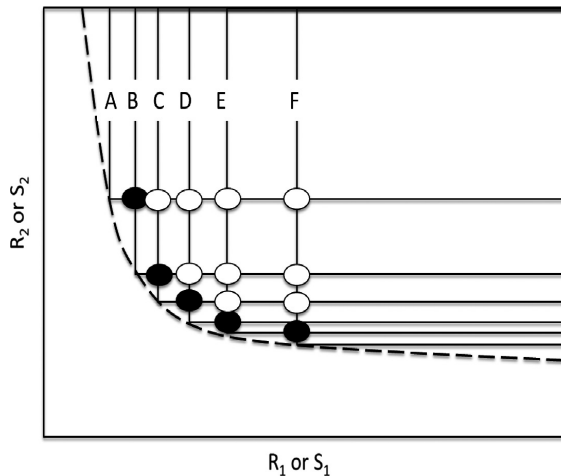
FIG. 4. Local community assembly in a metacommunity with six species that differ in their position on the R_{opt} gradient (different preferred resource supply ratios) compete at local sites that can consist of pairs of species (with consequent resource levels described by dots) or as single species (with consequent resource levels along their respective ZNGIs). Uninvasible local communities consist of pairs of species with adjacent positions along the R_{opt} gradient (with consequent resource levels shown as filled circles) or of single species closest to the R_{opt} constraint (dashed line). These are possible endpoints to community assembly. Other possible local communities (pairs of species with non-adjacent positions along the R_{opt} constraint or single species more distant from the R_{opt} line) are possible but are not endpoints for community assembly. Any community inhabited by one of these non-endpoint communities has higher resources levels than the equivalent endpoint.

additions, the relationship between species richness and ecosystem function (measured as community biomass) was no longer significantly positive; and a negative richness-biomass relationship (similar to that documented by Rychtecká et al. 2014; Fig. 3) emerged after several years. In this case, it is hard to know without further analysis if spontaneous invasion/seed addition caused a dispersal sufficiency or dispersal surplus scenario, but this example clearly shows how the original dispersal limitation scenario (communities closed to immigration) resulted in a different biodiversity-ecosystem function relationship.

COMBINED DISPERSAL LIMITATION AND ENVIRONMENTAL CHANGE

One important consequence of a dispersal-limited metacommunity is how it responds to environmental change. Leibold and Norberg (2004) used models similar to those we use here to show that altering environmental supply rates should influence local diversity and ecosystem functioning with and without dispersal limitation. When there is local environmental change, dispersal limitation should reduce both local diversity and ecosystem functioning largely as a result of reduced selection effects—species best suited to the new local conditions are limited in their ability to disperse to newly suitable

habitat and the community cannot track the change in environment as easily as it can with dispersal (see also Mouquet et al. 2002, Thompson and Gonzalez 2016).

An empirical example of how dispersal limitation influences the recovery of communities and ecosystem functioning from external perturbations is illustrated by Baho et al. (2012), who studied how freshwater bacterioplankton communities respond to salinity perturbations. Experiments occurred in closed systems (chemostats), in systems with a temporal refuge (chemostats with a biofilm that protected bacteria from washout), and in systems open to immigration from a regional species pool (via immigration at 10% per day from the undisturbed treatment). There was little recovery even after 18 d (up to several hundred generations). However, the immigration treatments recovered more than the others, albeit incompletely. Stronger recovery with immigration suggests that dispersal from suitable habitats might enhance recovery from perturbations and, by extension, the ability of communities to track environmental changes. A number of other studies show similar lags in the resilience of ecosystems, even when inhabited by microbial (Berga et al. 2012, Declerck et al. 2012, Andersson et al. 2014) and planktonic (Naeslund and Norberg 2006, Verreydt et al. 2012, Symons and Arnott 2013) communities long thought to not be dispersal limited. They also occur in grasslands (Maron et al. 2014) where dispersal limitation is more likely.

The previously mentioned studies and our proposed conceptual framework suggest that local richness and ecosystem function could respond differently to environmental change. If the regional pool lacks species with suitable traits for the new environment, and/or dispersal limitation prevents the most suitable species from colonizing, then communities undergoing environmental change may become dominated by subdominant species (Fig. 1c). Because subdominant species contribute less to ecosystem function, it is possible (even likely) for local species richness to be highly robust to disturbance and environmental change even though species composition and resulting ecosystem functioning are much less so. Potential support for this can be found in a meta-analysis of 114 studies (Supp and Ernest 2014) that found that disturbance's influence on individual species and community composition was quite strong, its impact on total abundance (a crude measure of ecosystem function) was less strong, and species richness was the least affected of all. Thus, while far from definitive, the empirical evidence currently available suggests that dispersal-limited metacommunities and their ecosystem functions, warrant far more theoretical and empirical attention than they have received to date.

CONCLUSIONS

Over two decades of research on biodiversity effects on ecosystem functioning (Schulze and Mooney 1994) has influenced how we think about the value of biodiversity and its contribution to ecosystem services. The wealth of
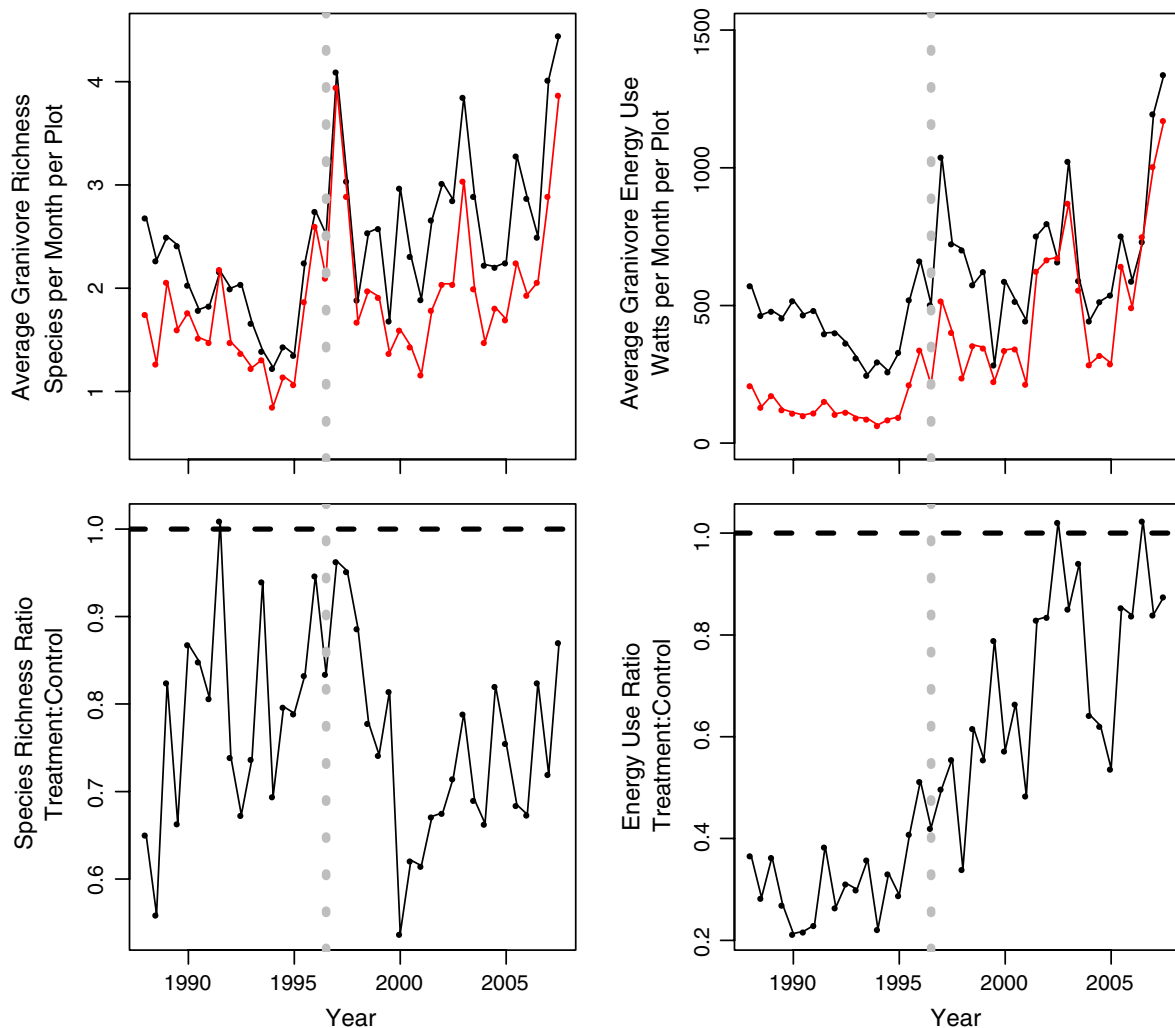
Fig. 5. Responses of total granivore species richness (left panels) and energy use as a measure of ecosystem function (right panels) in experimental plots in which *Dipodomys* sp. were removed (red symbols) compared to controls (black symbols) through time. The data is separated into two sections by the gray dashed line denoting the arrival of *Chaetodypus baileyi* to the site. The upper panels show the raw data, the lower panels express the same data as the ratio of the control to removal treatments. See Thibault et al. (2010) for details.

studies in different systems conducted by different researchers using a variety of approaches has shown that biodiversity and the functioning of ecosystems are linked, at least at some spatial scales (Cardinale et al. 2012, Hooper et al. 2012, Naeem et al. 2012, Tilman et al. 2014, Grace et al. 2016). However, these studies focus largely on the local level (small plots, chemostats, mesocosms), creating a gap in our understanding of how regional processes influence both biodiversity and ecosystem function through community assembly. A major limitation of current BEF research is that high rates of anthropogenic losses in biodiversity at the global scale (e.g., Ceballos et al. 2015) are often assumed to generate losses of biodiversity at the small scales on which BEF relationships occur. Justifications for conservation of biodiversity based on ecosystem functioning then unduly rely on the premise that local biodiversity is similarly declining

(Srivastava and Vellend 2005). While there is certainly some evidence for local biodiversity losses, especially in the face of anthropogenic change (Murphy and Romanuk 2014, Newbold et al. 2015), local diversity in a many ecosystems has remained stationary for decades, and has even increased in some (Vellend et al. 2013, Dornelas et al. 2014, Elahi et al. 2015), even when local communities are perturbed (Supp and Ernest 2014). We argue that a narrow focus on local BEF relations is insufficient to address emerging questions about the broader processes that link community assembly to the functioning of ecosystems (CAFÉ) and that a larger-scale (i.e., metacommunity) perspective is the next step toward improving our understanding of the role of biotas on ecosystem processes.

So, how does dispersal within a metacommunity affect local community assembly and consequent relationships
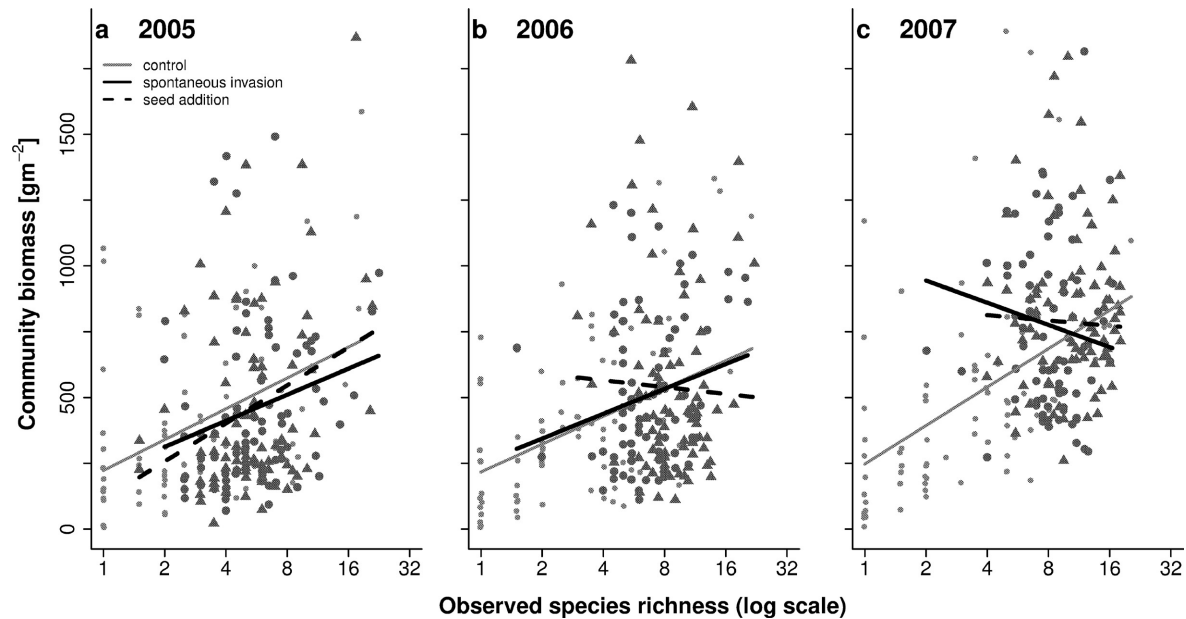
FIG. 6. Regressions of total community biomass (y-axis) against observed species richness (x-axis) in the Jena biodiversity experimental plots. Light grey small dots and thin grey solid line correspond to "closed" (labeled "control") biodiversity plots where biodiversity was experimentally maintained via weeding. Dark grey larger dots and solid black line correspond to plots that were initially the same as the control plots, but where weeding was stopped in 2005 (labeled "spontaneous invasion"). Dark grey triangles and dashed black line correspond to plots in which an even mixture of seeds from 60 species were added in 2005 (labeled "seed addition"). Figure modified from Petermann et al. (2010).

between biodiversity and ecosystem function? Here we have argued that dispersal sufficiency, favored by intermediate levels of dispersal, leads to maximized ecosystem function at the local scale. It is tempting to link this effect with the prediction of intermediate peaks in local diversity in relation to dispersal (Mouquet and Loreau 2003). However the theory reveals that these peaks are not likely to be congruent; the peak in ecosystem function occurs when species sorting is maximized whereas the peak in diversity occurs at progressively higher dispersal when it creates source-sink relations among local communities that differ in local environmental conditions. This conclusion is confirmed by recent theoretical work using simulations of resource competition in metacommunities (Thompson and Gonzalez 2016). Our models do not make clear predictions about relationships between local diversity and ecosystem functioning and indeed such relationships at the local scale are weak at best (e.g., Grace et al. 2016). On the other hand, our model predicts that high regional diversity should be correlated with enhanced mean local ecosystem functioning, a pattern that generally seems much stronger (Grace et al. 2016). Here we argue that this could be due to variation in dispersal and disturbance, but other models argue that these predictions may also result from other ecological processes involving environmental variation and heterogeneity (Grace et al. 2016).

Many of the concepts that we present have been present in the literature for some time (Mouquet et al. 2002, Loreau et al. 2003, Mouquet and Loreau 2003, Gonzalez et al. 2009, Livingston et al. 2012, Shanafelt et al. 2015,

Thompson and Gonzalez 2016). We have attempted to synthesize these ideas to highlight the importance of community assembly processes in mediating biodiversity ecosystem function relationships, focusing specifically on the influence of spatial processes (i.e., metacommunity dynamics) on resource-competition structured communities. Importantly, spatial processes can also impact the trophic structure of communities (e.g., Allhoff et al. 2015) which in turn can potentially alter biodiversity-ecosystem function relationships (Poisot et al. 2013, Allhoff and Drossel 2016). The general framework we have laid out necessarily avoids some of the complexities involved when trophic interactions are also influenced by spatial processes, and influence ecosystem functioning. And thus, our framework serves only as a starting point to motivate research toward a common framework for considering how community assembly influences biodiversity and ecosystem function across both temporal and spatial scales.

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CONCEPTS & SYNTHESIS