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## **The promise and pitfalls of beta diversity in ecology and conservation**

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### **Abstract**

A key challenge in ecology and conservation is to determine how processes at different scales create variation in community composition ( $\beta$ -diversity). In this issue, Oldén & Halme show that grazers increase  $\beta$ -diversity through multiple processes at different scales. We discuss how  $\beta$ -diversity can elucidate fundamental processes of community assembly, challenges in linking processes to patterns, and unresolved questions across scales.

Understanding the processes determining variation in community composition through space and time ( $\beta$ -diversity) is a fundamental pursuit in ecology, evolution and conservation.

Studies of  $\beta$ -diversity examine many different levels of biological organization, spanning

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variation in species, functional-trait, and phylogenetic composition both within and across trophic levels. As a scalar that links patterns of diversity across local and regional scales,  $\beta$ -diversity can inform conservation and provide insights into fundamental processes underlying the assembly, diversity and dynamics of communities. In this issue, Oldén & Halme (2016) illustrate the value of  $\beta$ -diversity to both theory and conservation. First, they find that grazers can cause scale-dependent changes in  $\beta$ -diversity through herbivory and by altering environmental heterogeneity. Second, their results have important conservation implications for the management of biodiversity in human-altered landscapes. In this commentary, we highlight the promise and pitfalls of  $\beta$ -diversity in ecology and conservation.

#### **How can $\beta$ -diversity provide insights into the big four processes in community ecology?**

Ecological communities are envisaged as the product of four fundamental processes: speciation, dispersal, niche selection, and ecological drift (Vellend 2010). These four processes can individually and interactively determine  $\beta$ -diversity by shaping the relative abundances of species at local and regional scales (Fig. 1). Speciation and dispersal influence the number of species in the regional species pool. In regions with larger species pools, a smaller fraction of the species pool is expected to occur in any one locality, resulting in higher  $\beta$ -diversity (Kraft et al. 2011). At local scales, niche selection can either decrease or increase  $\beta$ -diversity (Chase & Myers 2011). For example, a strong environmental filter, such as drought or natural enemies (e.g. predators, pathogens), can homogenize community composition (lower  $\beta$ -diversity) by selecting for species with drought- or enemy-tolerant traits. In contrast, different abiotic or biotic conditions among communities can increase  $\beta$ -diversity by selecting for species with different traits. Importantly, processes can interact in complex ways to influence  $\beta$ -diversity. Increased dispersal can homogenize communities if selection is relatively weak (Hubbell 2001). In contrast, dispersal can either decrease or

increase  $\beta$ -diversity if selection is strong. For example, if species differ in their competitive ability or tolerance to natural enemies, dispersal can decrease  $\beta$ -diversity through mass effects (Mouquet & Loreau 2003). Alternatively, if species differ in their habitat requirements, dispersal could increase  $\beta$ -diversity via species sorting across abiotic or biotic gradients. In addition to deterministic mechanisms of community assembly, random changes in species relative abundances (ecological drift) can increase  $\beta$ -diversity in the absence of other processes (Hubbell 2001). Local drift, selection and dispersal can also feedback to structure the size and composition of the regional species pool (Mittelbach & Schemske 2015), with important consequences for  $\beta$ -diversity (Kraft et al. 2011).

### **Challenges in linking process to pattern**

Despite the appeal of using  $\beta$ -diversity to understand mechanisms of community assembly, many potential pitfalls line the path from process to pattern. First, dispersal, selection, and drift can create similar patterns of  $\beta$ -diversity (Myers et al. 2013). In these cases, additional mechanistic approaches are needed to disentangle the relative role of different processes. These include experiments that manipulate the process(es) of interest, null models that eliminate the process of interest, and analyses that relate variation in community composition to speciation, dispersal, selection and drift (e.g. partitioning biogeographic, environmental, and spatial influences on  $\beta$ -diversity) (Chase & Myers 2011).

Second, a bewildering array of  $\beta$ -diversity metrics exists. Many are not independent of other components of community structure, including the number of individuals in local communities (community size), local diversity ( $\alpha$ -diversity), regional diversity (e.g.  $\gamma$ -diversity) and the relative abundances of species in the regional species pool. Two common solutions to this problem include the use of  $\beta$ -diversity metrics that are relatively insensitive

to these components and the use of null models. Substantial debate in the literature has focused on which is the “best”  $\beta$ -diversity metric or null model. This debate often overlooks the fact that different  $\beta$ -diversity metrics and null models provide complementary information (Anderson et al. 2011; Mori et al. 2015). Moreover, a variety of  $\beta$ -diversity metrics or null models can be used in combination to test alternative hypotheses. For example, null models that vary the definition of the regional species pool (e.g. by including "dark diversity") can be used to test the influence of regional and local mechanisms on community assembly and  $\beta$ -diversity (Fig. 1). Ultimately, the  $\beta$ -diversity metric(s) and null model(s) used should be tailored to the question(s) at hand.

Third, patterns of beta diversity are scale-dependent. This is nicely illustrated by Oldén & Halme (2016), who examine patterns of  $\beta$ -diversity at three different spatial scales: (1) among small plots at local scales, (2) within grazing pastures, and (3) among grazing pastures. As in other studies that have explicitly examined  $\beta$ -diversity across scales,  $\beta$ -diversity patterns at different scales appear to result from different processes (Barton et al. 2013). These studies highlight that no single “best” scale exists at which to measure  $\beta$ -diversity and that useful insights can be gained by examining  $\beta$ -diversity at multiple scales.

### **Three examples of unresolved questions at different scales**

*1. How do species interactions across trophic levels influence  $\beta$ -diversity?* Empirical studies have largely focused on how species interactions within trophic levels influence  $\beta$ -diversity. More studies are needed that examine how species interactions across trophic levels (e.g. predation, mutualism) influence  $\beta$ -diversity, particularly through their influence on the relative importance of selection, dispersal and ecological drift. Oldén & Halme (2016) provide an example of how grazers may increase  $\beta$ -diversity through niche selection

(environmental heterogeneity via trampling) and dispersal (seed dispersal via dung). An alternative mechanism by which natural enemies could influence  $\beta$ -diversity is ecological drift. The extent to which natural enemies influence  $\beta$ -diversity via drift or selection may depend on the extent to which enemies are generalists or specialists. For example, specialized enemies may decrease  $\beta$ -diversity via negative frequency-dependent selection (Terborgh 2015). Alternatively, generalist enemies may increase  $\beta$ -diversity by decreasing community size and increasing the relative influence of demographic stochasticity (Orrock & Fletcher 2005). Moreover, even less is known about how processes within trophic levels scale up to influence variation in species-interaction networks (interaction  $\beta$ -diversity) and consequences for ecosystem services (Burkle et al. 2016).

2. *When do local versus regional influences on  $\beta$ -diversity matter most?* Classic models often depict community assembly as a top-down process from the regional species pool to local communities (Fig. 1, open arrow), as in mainland-island models. However, selection, drift and dispersal at local scales can feedback in a bottom-up way to influence the regional species pool (Mittelbach & Schemske 2015). A promising area of future research is to determine the conditions under which such bottom-up feedbacks most strongly exert local control over regional components of diversity (Fig. 1, hatched arrow).

3. *What are the processes that create and maintain  $\beta$ -diversity at continental to global scales?* Multiple processes acting at different scales influence global patterns of biodiversity, yet the relative importance of these mechanisms remains unresolved. In particular, little is known about how dispersal, selection, and drift at local scales contribute to patterns of  $\beta$ -diversity (within or across trophic levels) across biogeographic regions that differ in their speciation, extinction and dispersal histories (Myers et al. 2013).

## Conclusions

We have highlighted some of the promises and challenges of integrating  $\beta$ -diversity into community ecology theory. However,  $\beta$ -diversity is also important for conservation, management and restoration because it describes how communities respond to anthropogenic influences and environmental change at different scales. Many restoration and management practices focus on maximizing local ( $\alpha$ ) diversity. Yet, as Oldén & Halme (2016) show, some management practices (e.g. introduction of grazers) can increase  $\beta$ -diversity and thus maximize diversity at larger spatial scales that are increasingly germane to conservation. Studies such as these demonstrate the value of understanding how processes at different scales interact to determine community assembly and inform the management and conservation of biodiversity in changing landscapes.

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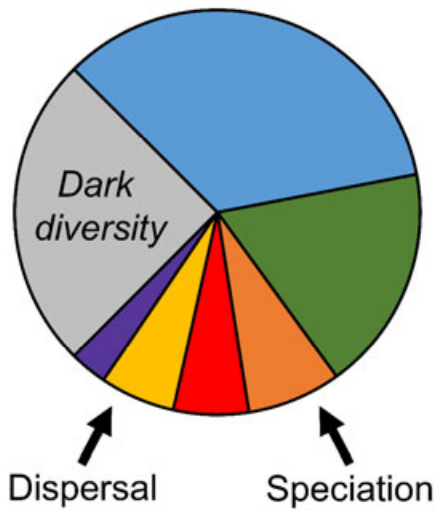
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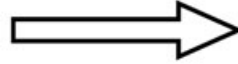
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## Regional Species Pool

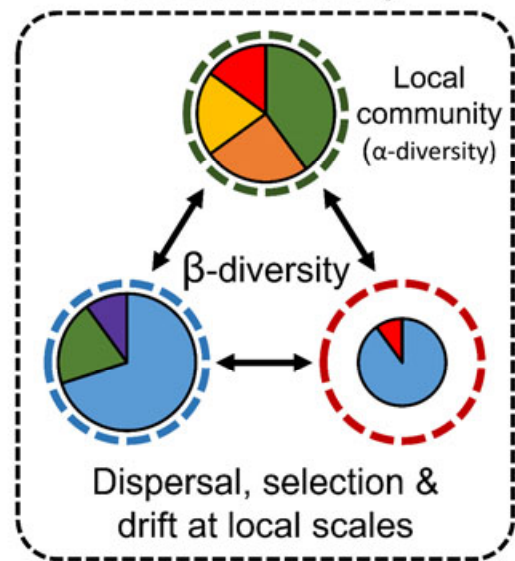


Regional effects  
on local  
communities



Local effects  
on the regional  
community

## Metacommunity



**Fig. 1.** Conceptual framework for the influence of speciation, dispersal, niche selection, and ecological drift on community assembly and  $\beta$ -diversity. Speciation and dispersal influence the number and relative abundances of species in the regional species pool. Dispersal from the regional pool (open arrow) adds individuals to local communities. Within the metacommunity, dispersal among localities along with selection and drift within localities influence local numbers of species ( $\alpha$ -diversity) and variation in community composition ( $\beta$ -diversity). Dashed colored circles around localities represent different ecological conditions (e.g. abiotic conditions, predation, competition) that select for particular traits or species. The influence of drift may override selection when community size (pie-chart size) is small (e.g. lower-right community). Local dispersal, selection and drift can also feedback (hatched arrow) to influence the size and composition of the regional species pool and speciation rates (Mittelbach & Schemske 2015). Pie-charts represent regional (left) or local communities (right), colors represent different species, and the size of slices represent relative abundances of species. Regional species pools are commonly defined as the total number of species sampled across local communities ( $\gamma$ -diversity), but this definition overlooks species not sampled in focal communities but nonetheless present in the region, or “dark diversity” (Pärtel et al. 2011).