RESEARCH ARTICLE

AMERICAN JOURNAL OF BOTANY

INVITED PAPER

For the Special Issue: Evolutionary Insights from Studies of Geographic Variation

The beta-diversity of species interactions: Untangling the drivers of geographic variation in plant–pollinator diversity and function across scales[1]

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PREMISE OF THE STUDY: Geographic patterns of biodiversity have long inspired interest in processes that shape the assembly, diversity, and dynamics of communities at different spatial scales. To study mechanisms of community assembly, ecologists often compare spatial variation in community composition (beta-diversity) across environmental and spatial gradients. These same patterns inspired evolutionary biologists to investigate how micro- and macro-evolutionary processes create gradients in biodiversity. Central to these perspectives are species interactions, which contribute to community assembly and geographic variation in evolutionary processes. However, studies of beta-diversity have predominantly focused on single trophic levels, resulting in gaps in our understanding of variation in species-interaction networks (interaction beta-diversity), especially at scales most relevant to evolutionary studies of geographic variation.

METHODS: We outline two challenges and their consequences in scaling-up studies of interaction beta-diversity from local to biogeographic scales using plant–pollinator interactions as a model system in ecology, evolution, and conservation.

KEY RESULTS: First, we highlight how variation in regional species pools may contribute to variation in interaction beta-diversity among biogeographic regions with dissimilar evolutionary history. Second, we highlight how pollinator behavior (host-switching) links ecological networks to geographic patterns of plant–pollinator interactions and evolutionary processes. Third, we outline key unanswered questions regarding the role of geographic variation in plant–pollinator interactions for conservation and ecosystem services (pollination) in changing environments.

CONCLUSIONS: We conclude that the largest advances in the burgeoning field of interaction beta-diversity will come from studies that integrate frameworks in ecology, evolution, and conservation to understand the causes and consequences of interaction beta-diversity across scales.

KEY WORDS behavioral plasticity; biodiversity–ecosystem function; biogeographic gradient; community assembly; conservation; environmental gradient; interaction turnover; plant–pollinator network; pollination services; species pool

Spatial patterns of biodiversity have inspired natural historians, ecologists, and evolutionary biologists for over a century (Arrhenius, 1921; Fisher et al., 1943; Dobzhansky, 1959; Whittaker, 1972; Watson, 1859 in Rosenzweig, 1995; Anderson et al., 2011). Some of the most striking patterns in biodiversity observed by early naturalists included declines in species richness with increasing latitude and elevation (Pianka, 1966; Hillebrand, 2004; Rahbek, 2005). More recently, ecologists have differentiated between alpha-diversity (local diversity), beta-diversity (site-to-site variation in community composition), and gamma-diversity (regional diversity) to better understand the processes that structure communities at different spatial scales. In particular, beta-diversity has become a foundational concept used to address questions at the interface of biogeography, community ecology, and evolutionary biology (Graham and Fine, 2008; Anderson et al., 2011; Chase and Myers, 2011). As a measure of how community composition changes from local to regional scales, beta-diversity can provide key insights into the processes that create and maintain geographic gradients of biodiversity (e.g., Condit et al., 2002; Tuomisto et al., 2003; Kraft et al., 2011; Tello et al., 2015). Moreover, beta-diversity is increasingly used by ecologists to inform conservation and restoration of communities altered

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[1] Manuscript received 28 February 2015; revision accepted 6 July 2015.

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doi:10.3732/ajb.1500079

by anthropogenic disturbance (Vellend et al., 2007; Chalcraft et al., 2008; Grman and Brudvig, 2014), changes to natural disturbance regimes (Myers et al., 2015), and climate change (Leprieur et al., 2011).

Despite decades of interest in the causes and consequences of beta-diversity, the vast majority of theoretical and empirical studies have focused on patterns of beta-diversity within single trophic levels. Concurrently, there has been a surge of interest in using species-interaction networks to understand how ecological and evolutionary processes shape communities of interacting trophic levels (Bascompte and Jordano, 2007; Vázquez et al., 2009; Sutherland et al., 2013). Little is known, however, about how the properties of ecological networks vary across space and time (e.g., de Ruiter et al., 2005; Burkle and Alarcón, 2011). As a result, there are fundamental gaps in our understanding of the beta-diversity of species interactions, especially at large spatial and temporal scales most relevant to evolutionary studies of geographic variation (Box 1). Variation in species-interaction networks across sites and through time, known as interaction beta-diversity (or as interaction turnover), may provide unique insights into mechanisms of community assembly, species coexistence, and the responses of trophic interactions and emergent ecosystem services to global change (Novotny, 2009; Tylianakis et al., 2010; Burkle and Alarcón, 2011; Fontaine et al., 2011; Poisot et al., 2012, 2014; Simanonok and Burkle, 2014).

Although it may be tempting to rapidly transition from single to multi-trophic studies of beta-diversity, we suggest that many of the fundamental problems that have long plagued studies of beta-diversity in single trophic levels will also present fundamental challenges as ecologists begin to scale-up to interaction beta-diversity. In this paper, we build on recent advances in our understanding of beta-diversity within and across trophic levels to develop a mechanistic framework for studies of interaction beta-diversity at local and biogeographic scales. We outline two fundamental challenges in scaling-up interaction beta-diversity from local to biogeographic

Box 1. Examples of outstanding questions in studies of interaction beta-diversity at local and biogeographic scales.

Regional and local influences on interaction beta-diversity

1. What are the spatial and temporal scales of variation in species pools of interacting trophic levels? Understanding the spatiotemporal scales at which species pools of different trophic levels vary will provide insight into the scales at which interaction beta-diversity may be important for community function and the relative importance of drivers of interaction beta-diversity across complex landscapes.
2. What ecological conditions determine the relative importance of regional and local influences on interaction beta-diversity? Studies that identify (1) when each of the proximate drivers of interaction beta-diversity is relatively more important, (2) relationships among the drivers, and (3) relationships between interaction beta-diversity and environmental gradients will help resolve this question. For example, we might expect host-switching to be more important for interaction beta-diversity at small spatial scales, whereas beta-diversity within trophic levels may be more important for interaction beta-diversity at larger spatial scales.
3. Do similar processes drive clumping of species across trophic levels? Dispersal limitation and habitat filtering are commonly invoked to explain clumping of plant species (McGill, 2010). However, little is known about the relative importance of these and other mechanisms between trophic levels. For example, the spatial distribution of both floral resources and nesting resources is understudied for pollinators and would enable predictions about the spatial scale of pollinator clumping and beta-diversity. In addition, for pollinators that use different plant resources over the course of their lives (e.g., butterflies), to what degree does the clumping of resources used at early life-history stages contribute to or differ from clumping at later life-history stages?

Context dependency of host-switching

4. Under what conditions is host-switching most likely to take place? Behavioral energetics, optimal foraging theory, and competition may be useful in predicting thresholds of resource quantity, quality, and spatial distribution where host-switching is exhibited.
5. What are the consequences of host-switching for coevolutionary processes and the evolution of traits across different communities? Placing individual behaviors within a community context will help advance our understanding of the functional consequences of host-switching in an evolutionary context.

Consequences of interaction beta-diversity for management and conservation

6. What are the consequences of variability in interaction beta-diversity for ecosystem services? For example, few studies have compared how individual pollinator behavior (i.e., fidelity), plant–pollinator network structure, and pollination services vary across heterogeneous landscapes. Geographically replicated experiments on pollen limitation (e.g., Ashman et al., 2004; Knight et al., 2005) may be especially useful for assessing how interaction beta-diversity influences pollination services.
7. How can interaction beta-diversity help inform management decisions for natural and human-modified ecosystems? Investigation of fitness feedbacks between plants and pollinators may help determine the conditions under which high, stable pollination services can be maintained through time at the landscape level, even if some populations within the landscape have suboptimal pollination.

scales and highlight the consequences of these challenges for conservation and management. First, we highlight key lessons that have been learned from studies of beta-diversity in single trophic levels to help guide the development of the burgeoning field of interaction beta-diversity. In particular, we emphasize how variation in regional species pools (gamma-diversity) may contribute to variation in interaction beta-diversity among biogeographic regions with dissimilar evolutionary history. Second, we illustrate how geographic variation in individual behavior (host-switching) may influence interaction beta-diversity using plant–pollinator networks as a model system in ecology, evolution, and conservation. We suggest that explicit consideration of pollinator behavior is necessary to link ecological networks within communities to geographic patterns of plant–pollinator interactions as well as to understand the outcomes of plant–pollinator interactions in an evolutionary context. We outline challenges associated with integrating individual behavior into species-interaction networks, most of which generally consider behavior to be a static property of a species (Poisot et al., 2014). These challenges may be particularly acute in studies of plant–pollinator networks, where recent evidence suggests that there is daily, seasonal, and interannual variation in these networks at local scales (e.g., Olesen et al., 2008; Baldock et al., 2011; Simanonok and Burkle, 2014). Finally, we highlight key unanswered questions regarding the role of geographic variation in plant–pollinator interactions in the conservation and management of ecosystem services (pollination) in changing environments.

SCALING-UP FROM LOCAL TO BIOGEOGRAPHIC SCALES: TWO FUNDAMENTAL CHALLENGES

Challenge 1: Regional and local influences on interaction beta-diversity—A ubiquitous challenge in ecology and evolutionary biology is to disentangle how multiple processes acting at different scales combine to shape observed patterns of biodiversity. Although patterns of diversity have inspired a rich body of mechanistic theories in ecology and evolution (e.g., Hubbell, 2001; McGill, 2010), empirical approaches that rely on these patterns to infer mechanisms continue to fuel controversy over the underlying processes (Chave et al., 2002; Chase and Myers, 2011; Chase and Knight, 2013). This controversy emerges in part because dissimilar processes often create similar patterns of biodiversity in natural communities (Chave et al., 2002; Myers et al., 2013). For example, recent studies have suggested that observed patterns of beta-diversity are influenced by variation in at least four factors: (1) the number of individuals in local communities, or community size (Orrock and Fletcher, 2005; Chase and Myers, 2011; Myers et al., 2015); (2) the relative abundances of species (Chase and Knight, 2013); (3) the size of the regional species pool (Kraft et al., 2011); and (4) eco-evolutionary processes that influence spatial aggregation (clumping) of species (McGill, 2010, 2011). The realization that observed patterns alone may be insufficient for studying the drivers of beta-diversity has resulted in an explosion of interest in new quantitative approaches. These approaches include metrics of beta-diversity that are independent of variation in local (alpha) diversity (Jost, 2007; Chase et al., 2011), null models to compare beta-diversity among biogeographic regions where regional (gamma) diversity varies (Kraft et al., 2011; Myers et al., 2013; Tello et al., 2015), and frameworks that integrate functional, phylogenetic, and taxonomic dimensions of beta-diversity (Graham and Fine, 2008; Chao et al., 2014). Although debate persists regarding the limitations and merits of different approaches, these studies have provided valuable insights into the drivers of beta-diversity at biogeographic scales.

A key insight emerging from recent studies of beta-diversity is that compositional variation within trophic levels generally increases from low- to high-diversity regions (Koleff et al., 2003; Qian and Ricklefs, 2007; Soininen et al., 2007; De Cáceres et al., 2012). Although differences in community assembly mechanisms such as dispersal limitation, habitat filtering, and biotic interactions may contribute to this pattern, differences in the size of the species pool (gamma- diversity) among regions can create this pattern simply through a random sampling effect (Kraft et al., 2011). Thus, to discern potential sampling effects, it is necessary to use null-model approaches to compare observed patterns of beta-diversity to patterns expected from random sampling of the species pool (Kraft et al., 2011, De Cáceres et al., 2012; Stegen et al., 2013; Myers et al., 2013; Mori et al., 2015; Tello et al., 2015). A typical goal of these models is to simulate patterns of beta-diversity that would be expected in the absence of processes that create spatial aggregation (clumping) of species within communities assembled from observed species pools. Large deviations of observed patterns from the null model may therefore reflect an important role of community assembly processes that create clumping of species (Kraft et al., 2011). Small deviations of observed patterns from the null model, in contrast, may suggest that beta-diversity is driven more strongly by the regional species pool than local community processes. In these cases, biogeographic and evolutionary processes that create geographic variation in the size and composition of the regional species pool may play a more central role in determining patterns of beta-diversity (Ricklefs, 1987). Moreover, deviations from the null model can be partitioned across environmental and spatial gradients to test hypotheses regarding potential mechanisms of community assembly (Myers et al., 2013; Myers et al., 2015). Current evidence, primarily based on studies of plant communities (but see Stegen et al., 2013 for an example with birds), suggests that geographic gradients in beta-diversity can be strongly influenced by regional variation in species pools (Kraft et al., 2011; De Cáceres et al., 2012; Myers et al., 2013). These patterns suggest that regional variation in species pools may also be an important driver of observed patterns of interaction beta-diversity involving two or more trophic levels.

Despite growing interest in how species pools shape patterns of beta-diversity within trophic levels (Lessard et al., 2012; Cornell and Harrison, 2014), current models of interaction beta-diversity have yet to explicitly integrate species pools in a biogeographic context (Box 1). From a biogeographic perspective, species pools and local community assembly mechanisms can be envisioned as *ultimate* drivers of interaction beta-diversity that can influence or interact with several more *proximate* drivers of interaction beta-diversity (Fig. 1). Novotny (2009) developed a conceptual model for plant–herbivore food webs that includes four proximate drivers of interaction beta-diversity: (1) changes in the species composition of one trophic level (e.g., plants); (2) changes in the species composition of a second trophic level (e.g., herbivores or pollinators); (3) changes in the species composition of both trophic levels; and (4) changes in foraging behavior (host-switching) among sites. Although changes in any one of these proximate drivers will lead to changes in interaction beta-diversity, we show here with a simulation that interaction beta-diversity can be strongly influenced by geographic variation in species pools (Box 2). Thus, by explicitly

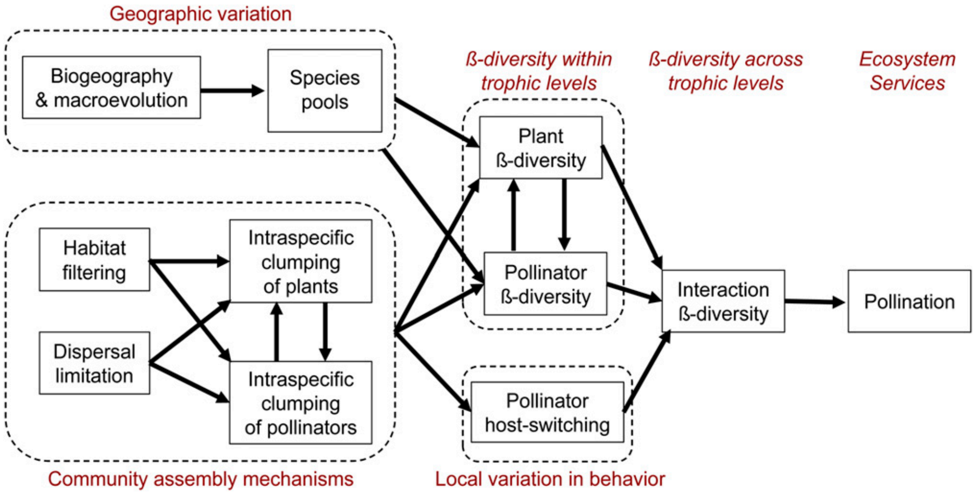

FIGURE 1 A conceptual model of the drivers of site-to-site variation in plant–pollinator networks (interaction beta-diversity) at local and biogeographic scales. Proximate drivers of interaction beta-diversity include variation in plant species composition (plant beta-diversity), pollinator species composition (pollinator beta-diversity), and pollinator host-switching. Each of these drivers reflects the outcome of two ultimate drivers: community assembly mechanisms and regional species pools. At local scales, community assembly mechanisms that increase spatial aggregation (clumping) of plant or pollinator species (e.g., dispersal limitation or habitat filtering) can increase beta-diversity within trophic levels. At biogeographic scales, variation in the size and composition of regional species pools also influences beta-diversity within trophic levels. A key challenge in studies of interaction beta-diversity is to understand how these drivers combine to influence critical ecosystem services such as pollination (Box 1).

integrating geographic variation in species pools into studies of interaction beta-diversity, we can begin to untangle the relative importance of different processes that contribute to variation in species interactions across local and biogeographic scales.

Challenge 2: Context dependency of host switching—A second major challenge in scaling-up studies of interaction beta-diversity from local to biogeographic scales is to understand how behavior and host-switching varies geographically. In this section, we illustrate this challenge using plant–pollinator networks. To understand the role of pollinator host-switching behavior as a proximate driver of interaction beta-diversity (Fig. 1) and its role in the ability of communities to respond to environmental change, we briefly review evolutionary, behavioral, and community perspectives on the study of plant–pollinator interactions. We also underscore the contributions or limitations of each perspective for understanding variation across biogeographic scales or through time.

The idea that pollinators can contribute to, and even strongly steer, the evolution of flowering plant diversity can be traced back to Darwin (1859, 1877). Tight coevolutionary processes (sensu Ehrlich and Raven, 1964) between plants and their pollinators as well as pollination syndromes led to the perspective that plant–pollinator interactions are specialized. This perspective has shifted over time, with recognition that few plant–pollinator interactions are truly specialized, while the majority are relatively generalized (Waser et al., 1996). Given broad, and not fully overlapping, biogeographic ranges of plants and pollinators in combination with limited membership of local communities, coevolution is likely diffuse, resulting in reciprocal evolutionary change among groups of species rather than between specific pairs (Janzen, 1980; Schemske, 1983). Studies of selection in this context are often plant-centric, focusing on floral traits and consequences for pollinator attraction and plant reproduction in different environments (e.g., Bertsch, 1983; Rathcke, 1992; Geber and Moeller, 2006; Harder and Johnson, 2009; Mitchell et al., 2009). In a complementary manner, studies of pollinator behavior have often focused on the foraging behavior of individuals in relation to the availability of floral rewards from one or a few plant species (e.g., Zimmerman, 1983; Goulson, 1999). Early studies made great progress in advancing the field of optimal foraging theory (reviewed in Pyke, 1984), but have lagged at solidifying critical connections to community ecology (e.g., Aigner, 2006; Mittelbach, 2012). Only recently have there been theoretical attempts to integrate the foraging behavior of pollinator individuals with implications for the dynamics, coexistence, and structure of simple communities (Rodríguez-Gironés et al., 2010; Song and Feldman, 2014).

Conceptualizing plant–pollinator interactions as ecological networks of species in communities is an approach complementary to, but often disjunct from, that of behavioral and evolutionary biologists. Until recently, interactions among species in a network were treated as static and inflexible. Representing interactions as static is particularly problematic when attempting to characterize and compare interactions across large spatiotemporal scales, as is the case for biogeographic gradients in plant–pollinator interactions and interaction beta-diversity. Increasingly, ecologists are recognizing that the maintenance of ecosystem services, like pollination, require an understanding of not only the species that are present at a location but also how they interact in that particular community context. Two species that are known to interact with each other at one location may not necessarily interact with each other at another location, even when they co-occur in space and have overlapping phenologies. Thus, merely knowing the suites of species present at a location may be insufficient to infer their patterns of interactions and the quality of resulting pollination services. The idea that the identities and outcomes of species interactions are contingent on community context is certainly not a new one (e.g., Bronstein, 1994; Tylianakis et al., 2010; Chamberlain et al., 2014), but has been slow to be incorporated into the measurement and interpretation of ecological networks. Fortunately, pollinator diet breadth is increasingly recognized as a flexible trait in the context of ecological networks (Fontaine et al., 2008; Kaiser-Bunbury et al., 2010; Burkle et al., 2013; Poisot et al., 2014), and this shifting perspective will facilitate the connections between individual pollinator behavior, community interaction networks, and pollination services across landscapes (Box 1).

It is important to emphasize that individual behaviors—such as foraging patterns of individual pollinators—are directly related to evolutionary processes, reproduction, and population dynamics (e.g., Brosi and Briggs, 2013; Tur et al., 2013, 2014; Dupont et al.,

Box 2. A modeling exercise to examine how changes in species-pool size and community size may influence patterns of interaction beta-diversity

Patterns of beta-diversity within trophic levels may be strongly influenced by random sampling effects resulting from variation in the size of the regional species pool (gamma-diversity) and variation in the numbers of individuals in local communities (community size) (Chase and Myers, 2011; Kraft et al., 2011; Myers et al., 2015). Similarly, we expect patterns of interaction beta-diversity to vary with the size of the species pool and local community size. In particular, we expect (1) interaction beta-diversity to increase as the size of the species pool increases owing to stronger sampling effects in species-rich regions compared with species-poor regions, and (2) the sampling effect to decrease as community size increases (i.e., as the total number of individuals in local communities approaches the total number of individuals in the regional pool).

To examine these predictions, we used a simple simulation model to randomly assemble local communities of plants and pollinators from regional species pools that vary in gamma-diversity (N = 10 communities in each region). In each simulation, we assembled local communities by randomly sampling individuals from the regional species pool while preserving the relative abundance of each species in the regional pool and the total number of individuals in each community. Plants and pollinators were modeled to interact based on their combined abundances in the community. In other words, rare species interacted with common species, and common species interacted with each other, but rare species interacted very infrequently with each other, thus creating a nested interaction network structure commonly observed in natural communities (e.g., Bascompte et al., 2003). Within each region, mean interaction beta-diversity was calculated as $b + c / a + b + c$, where a is the number of interactions shared between two networks, b is the number present only in the first network, and c is the number present only in the second (i.e., complementary to Jaccard's similarity index, Novotny, 2009), for all pairwise community comparisons. Simulations were repeated for regions that varied in gamma-diversity of plant species (50–500 species in a region) and for each of four different community sizes within each region: 500, 1000, 2000, or 4000 total plant individuals in each community (Fig. 2). In Fig. 2A, the gamma-diversity of pollinators was fixed at 350 species, the total number of pollinators in each community was fixed at 300 individuals, and both plants and pollinators had uniform species-abundance distributions. In Fig. 2B, we simulated variation in pollinator gamma-diversity (50–500 species in a region) and community size (100–800 total pollinators in a community) using a log-normal species-abundance distribution (mean = 0, standard deviation = 1) for both plants and pollinators.

Our simulations illustrate how sampling effects alone may create geographic gradients in interaction beta-diversity (Fig. 2). In particular, the results suggest that interaction beta-diversity is expected to increase as the size of the regional species pool increases, especially for communities with small numbers of individuals, regardless of the species-abundance distribution. These results suggest that changes in local community size due to natural and anthropogenic disturbances or habitat loss could alter the null-expected interaction beta-diversity among communities in a region. In such cases, if observed patterns of interaction beta-diversity are being used to inform management plans aimed at the conservation of biodiversity, species interactions, and resultant ecosystem services (see Consequences below), then such recommendations may result in suboptimal outcomes unless null-expectations are taken into account. These results underscore the importance of exercising caution when inferring mechanistic drivers of interaction beta-diversity from observed patterns alone, especially when comparing patterns at biogeographic scales where species pools vary. In addition, they highlight the need for empirical and theoretical studies that explore how variation in local and regional abundances influences interaction beta-diversity (Mori et al., 2015; Myers et al., 2015). One way forward is to extend null models of beta-diversity developed for single trophic levels (e.g., Kraft et al., 2011; Myers et al., 2013) to studies of interaction beta-diversity at biogeographic scales (Box 1).

2014), By contrast, species-level patterns of interactions—such as generalization, or diet breadth, of pollinator species—help us understand how robust systems might be to perturbations (e.g., Bascompte et al., 2003; Tylianakis et al., 2010). For example, a generalist species of pollinator may have a wide diet breadth (i.e., visit many plant species) and play a central role in the community, but individuals of that species may specialize (i.e., have high fidelity to a plant species) (e.g., Kearns, 1992) and provide excellent pollination services. Differentiating between the interactions of a species in the context of ecological networks and the foraging behavior of individuals of that species in different community contexts will facilitate the accurate representation of interactions when comparing across different spatial and temporal scales and levels of biological organization. Furthermore, because the suites of species that co-occur and the relative trait distributions of those species likely vary in communities across complex landscapes, this perspective can also provide opportunities to understand coevolutionary hotspots in which reciprocal adaptation and fitness effects between interacting species occur (Thompson, 2005). Thus, individual behavior can link evolutionary ecology and population dynamics with functional traits, beta-diversity, ecological networks, and ecosystem services (Box 1).

Together, evolutionary, behavioral, and community perspectives can provide a powerful approach to investigating geographic variation in pollinator behavior and understanding its contribution to interaction beta-diversity. This union of fields has been proposed multiple times, beginning with Charles Elton (1927), and is no easy task. Given the recent rise of interest in understanding the role of host-switching in interaction networks and its functional consequences (e.g., Valdovinos et al., 2010, 2013; Ramos-Jiliberto et al.,

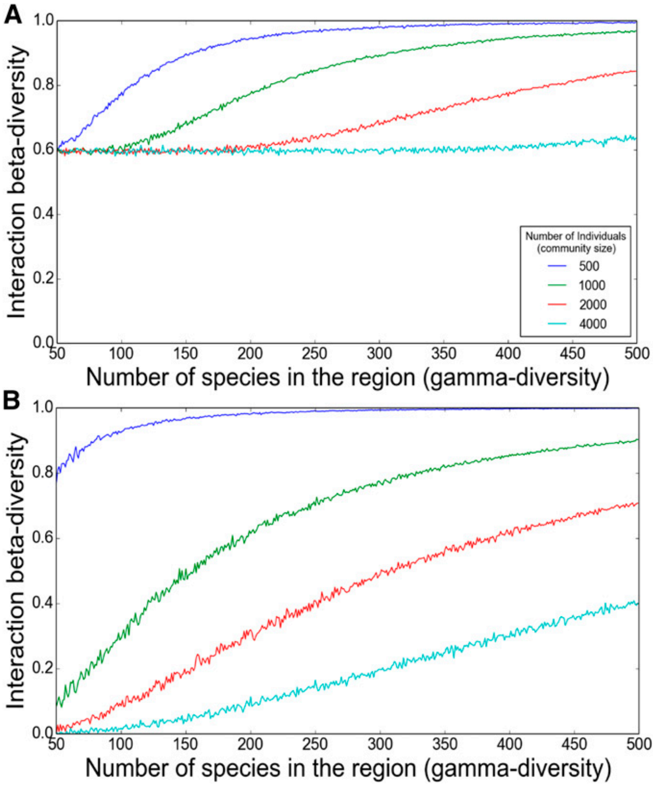

FIGURE 2 Relationships between mean interaction beta-diversity and the size of the regional pool (gamma-diversity) for different community sizes (total number of individuals in a community). The panels show results from simulations that varied the species-abundance distributions (SAD) in the regional species pool. Interactions between plants and pollinators are determined based on their combined abundances in the community (*N* = 5 individuals required for an interaction to occur). (A) Plants and pollinators have a uniform SAD. (B) Plants and pollinators have log-normal SADs. Mean interaction β-diversity was calculated as $b + c / a + b + c$, where a is the number of interactions shared between two networks, b is the number present only in the first network, and c is the number present only in the second, for all pairwise community comparisons.

2012; Simanonok and Burkle, 2014; Song and Feldman, 2014), we advise caution and critical thinking about the following questions as this field develops: (1) Under what spatial and temporal scales does host-switching contribute most strongly to interaction beta-diversity? (2) When does host-switching have the greatest potential to drive evolutionary processes and pollination services (Box 1)? Addressing these questions is essential to understand the maintenance and function of natural and managed systems.

SCALING-UP IN A CHANGING WORLD: CONSEQUENCES OF INTERACTION BETA-DIVERSITY FOR MANAGEMENT AND CONSERVATION

In the context of conservation and management, beta-diversity has been used to identify areas supporting unique species that may perform unique functions within ecosystems (e.g., Gering et al., 2003; Hewitt et al., 2005). Beta-diversity can also be used to indicate the spatial scale of landscape heterogeneity to infer the degree of redundancy in species' populations relative to the spatial scale of typical disturbances (e.g., Noss, 1983; Hobbs and Huenneke, 1992; Gabriel et al., 2006). Landscape-level redundancy in the occurrence of species' populations allows for some populations to be lost temporarily to disturbance or habitat loss while still maintaining the presence of that species in the region. If we extend this perspective on beta-diversity to interaction beta-diversity as well as its implications for conservation and management, we may find that our value system changes when the focus is shifted from species to species interactions. For example, although we may not value all species equally, we do place a high value on biodiversity and unique species, and we have mechanisms in place to protect threatened and endangered species (e.g., Pimm et al., 1995; Barlow et al., 2007; Mazzotti, 2014). Currently, however, we do not place the same value on unique species interactions. In fact, we often view species interactions as interchangeable and, perhaps, with good reason. A unique plant–pollinator interaction might be rare because the traits of the interacting individuals are poorly matched, the interactors do not receive benefits from the interaction in terms of pollination services or floral resources, or the interaction is selected against. Alternatively, a unique plant–pollinator interaction that is highly specialized and coevolved might be the object of conservation concern. Insights provided by interaction beta-diversity for conservation and management may not be as straightforward as insights gained from beta-diversity.

Geographic variation in studies of interaction beta-diversity may have many important, but largely unexplored, implications for conservation and management at large spatial scales (Box 1). Pollination, for example, is an emergent ecosystem service that results from ultimate and proximate drivers of interaction beta-diversity (Fig. 1) and exhibits variable quality across time and space (e.g., Knight et al., 2005). Agroecosystems have received the most attention thus far in terms of management practices that may maintain or enhance pollination as an ecosystem service (e.g., Klein et al., 2007; Carvalheiro et al., 2011; Garibaldi et al., 2014). Over short time-scales, maximum pollination of a crop species, for example, may be achieved by harnessing the services of one high-quality pollinator species (e.g., honey bees, *Apis mellifera*) in which individuals specialize and where populations can be maintained at high local densities. Specialized plant–pollinator interactions, however, may be sensitive to environmental fluctuations and pests or diseases that target crop or pollinator monocultures (e.g., Lin, 2011). Given recent declines in honey bees, our reliance on one species to fulfill our crop-pollination needs has highlighted the potential dangers of encouraging low-diversity systems through management (e.g., Garibaldi et al., 2011, 2013). Over longer time-scales, redundancy in pollinator species may buffer pollination services to changes in environmental conditions. Unfavorable conditions for some species may be favorable for others, yielding more reliable pollination under changing conditions when interaction beta-diversity is high compared with when it is lower. Studies are needed to determine whether interaction beta-diversity can provide managers of applied systems with a tool to gauge the likelihood of maintaining ecosystem services like pollination (Box 1).

Although it may be tempting to assume that interaction beta-diversity is always necessary to sustain ecosystem services like pollination, we urge ecologists and conservation practitioners to resist the temptation of focusing on the question "Is interaction beta-diversity good or bad?" Instead, we suggest that the causes and consequences of interaction beta-diversity have yet to be explored enough to provide useful guidance on the circumstances under which interaction beta-diversity may yield resilient or sustained pollination services in the face of environmental change (Box 1). Currently, it may be more useful to focus on determining *when* interaction beta-diversity is indicative of healthy ecosystems than to approach interaction beta-diversity through a bipolar lens. Focusing research in this way may be especially beneficial for the field of plant–pollinator networks, where the relationship between interaction beta-diversity and ecosystem services, like pollination, is largely unknown. This approach to interaction beta-diversity may allow for a richer understanding of why conservation goals and outcomes might vary across different biogeographic regions. In particular, future research may seek to advance our understanding of the *relationships among* and *relative contributions* of regional species pools, plant beta-diversity, pollinator beta-diversity, and host switching to interaction beta-diversity (Fig. 1; Carstensen et al., 2014; Simanonok and Burkle, 2014) across landscapes and through time (Box 1).

We highlight how interaction beta-diversity is relevant to plant-pollinator conservation using three examples: (1) disturbance, (2) habitat loss and fragmentation, and (3) changes in ecological processes across broad-scale environmental gradients.

Example 1. Disturbance—Among the many threats posed to biodiversity by global change, alterations in natural disturbance regimes are likely to have some of the most profound impacts on ecological communities and the ecosystem services they provide (Turner, 2010). Disturbance has been shown to increase (Belote et al., 2009; Vanschoenwinkel et al., 2013; Myers et al., 2015) or decrease (e.g., Chase, 2007; Passy and Blanchet, 2007; Vellend et al., 2007; Jiang and Patel, 2008; Lepori and Malmqvist, 2009; Myers and Harms, 2011) beta-diversity. Moreover, disturbance may more strongly influence the beta-diversity of some trophic levels over others. For example, theory suggests that higher trophic levels (pollinators) may be more susceptible to disturbance than lower trophic levels (plants) (Holt et al., 1999). Contrasting responses of plants and pollinators to disturbance, in turn, may strongly influence the extent to which patterns within trophic levels “scale up” to influence interaction beta-diversity (Novotny, 2009), the structure of interaction networks (Burkle and Alarcón, 2011), and essential ecosystem services such as pollination (e.g., Klein et al., 2007). Virtually nothing, however, is known about how disturbance influences interaction beta-diversity and pollination, especially at the large spatiotemporal scales most germane to conservation and management in dynamic landscapes (Turner, 1987).

Example 2. Habitat loss and fragmentation—Habitat loss and fragmentation threaten both species diversity and species interactions (e.g., Cagnolo et al., 2009; Laliberté and Tylianakis, 2010; Tylianakis et al., 2010). Only recently have we begun to explore how species-interaction networks are influenced by changes in land area (Sabatino et al., 2010; Sugiura, 2010; Burkle and Knight, 2012). Random sampling effects can alter species–area relationships (Preston, 1962), beta-diversity (Kraft et al., 2011), the accumulation of species interactions with habitat area (Burkle and Knight, 2012), and interaction beta-diversity (Box 2). To the extent that these results are general across ecosystems, larger habitats may be needed to conserve interactions and the accompanying pollination services than may be expected based on species-accumulation curves (Burkle and Knight, 2012).

In addition to potential effects of habitat loss on interaction beta-diversity, human modification of natural habitats is often biased toward high-quality habitats (Huston, 2005; Belote and Aplet, 2014). By contrast, we often conserve tracts of land that are less desirable for human use (Belote et al., 2011; Aycrigg et al., 2013), and these protected landscapes may contain only a subset of the original habitat types (c.f., Dietz et al., 2015) and may be poor in quality for some species. Habitat degradation can homogenize species interaction networks and alter the functional roles of species (Nielsen and Totland, 2014). Through reductions in habitat heterogeneity, habitat loss may differentially influence how species and interactions accumulate with area and, in turn, interaction beta-diversity. Furthermore, the distribution of habitat patches across the landscape and the degree of connectivity among them may influence interaction networks and interaction beta-diversity, especially for networks that include species or trophic levels with limited dispersal ability. Understanding the relationships between habitat area and quality, species richness and composition, and species interactions is crucial for the maintenance of biodiversity and ecosystem services across landscapes impacted by anthropogenic activities.

Example 3. Broad-scale environmental gradients—Geographic gradients in species richness are often correlated with broad-scale variation in abiotic factors such as climate, environmental heterogeneity, and net primary productivity (e.g., Hawkins et al., 2003; Hillebrand, 2004). Although the study of interaction networks across broad-scale gradients is still in its infancy (Novotny et al., 2006; Dyer et al., 2007; Dalsgaard et al., 2011; Schleuning et al., 2012; Morris et al., 2014; Trøjelsgaard et al., 2015), geographically replicated studies are especially germane to conservation and management of interaction networks and ecosystem services at large spatial scales. In particular, disturbance- and habitat-driven changes in beta-diversity and interaction networks may be strongly influenced by ecosystem productivity (e.g., Huston, 1979, 1994; Foster et al., 2004; McWethy et al., 2010). Within trophic levels, diversity has been observed to peak at low (Evans et al., 2008; Stegen et al., 2013), intermediate (Chalcraft et al., 2004), or high (Chase and Leibold, 2002; Chase, 2010; Belote et al., 2011) productivity, or show no relationship with productivity (Adler et al., 2011), suggesting variable influences of productivity on community assembly. Although little is known about how disturbance and productivity may interactively influence interaction beta-diversity, this knowledge could help inform conservation and management strategies across complex landscapes. For example, if productivity primarily influences interaction beta-diversity through its effect on the size of the species pool of plants or pollinators (Fig. 1, Box 2), then conserving regional biodiversity may be of critical importance for sustaining ecosystem services such as pollination. In contrast, if productivity primarily influences interaction beta-diversity by altering local, trophic interactions among species (Fig. 1, host-switching), then the maintenance of local environmental conditions that encourage structurally robust networks of plant–pollinator interactions could be targeted for conservation.

CONCLUSIONS AND OUTSTANDING QUESTIONS

In this paper, we described two fundamental challenges in scaling-up interaction beta-diversity from local to biogeographic scales. At the broadest spatiotemporal scales, we highlighted the importance of considering how geographic variation in regional species pools influences patterns of interaction beta-diversity (Fig. 1, Box 2). We then synthesized historical perspectives and recent literature on host-switching as a proximate driver of interaction beta-diversity and implications of host-switching for understanding geographic variation in natural selection and ecosystem services. Finally, we presented examples of how studies of interaction-beta diversity may be relevant for conservation and management.

Throughout the paper, we have highlighted several ways in which these non-mutually exclusive challenges may be integrated to help advance the study of interaction beta-diversity in an era of global environmental change, with a focus on plant–pollinator interactions. While the consequences of environmental change for plant–pollinator interaction beta-diversity may differ from other non-mutualistic species interactions or interactions within trophic levels, we expect the challenges associated with scaling up from local to biogeographic scales to be similar. Even so, several outstanding questions remain, largely owing to a paucity of empirical studies on patterns and mechanisms of interaction beta-diversity (Box 1). We find the unknown relationship between interaction beta-diversityand ecosystem services especially interesting. This field will be strongly advanced by investigation of the conditions under which interaction beta-diversity is beneficial and conservation of specific species interactions is realistic. We encourage future empirical research that investigates the causes and consequences of interaction beta-diversity to gain insights into community assembly, evolutionary outcomes, and ecosystem services across broad geographic scales.

ACKNOWLEDGEMENTS

The authors thank N. Soper Gorden, J. Bellemare, J. Etterson, S. Franks, C. Herlihy, H. Schneider, J. Sexton, and J. Weber for the opportunity to contribute to this special feature. The authors thank the National Science Foundation (DEB 1256788, 1256819) for financial support to perform research while developing these ideas. C. DeTar provided coding support for the simulation model. N. Soper Gorden, A. Iler, and one anonymous reviewer provided valuable comments on an earlier draft of this manuscript.

AUTHOR CONTRIBUTIONS

Statement of authorship: All authors conceived of the paper; L.B. and J.M. drafted the manuscript; L.B. performed the simulation model; all authors contributed to revisions.

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