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INVITED VIEWS IN BASIC AND APPLIED ECOLOGY

## Global change, biodiversity, and ecosystem services: What can we learn from studies of pollination?

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### Abstract

The study of global environmental change and its effect on biodiversity and ecosystem function is at an exciting crossroads, at which ideas developed largely through theory and small-scale experiments are now being tested with ecosystem services as they are delivered to people in real-world landscapes. Pollinators and pollination are emerging as a model system for exploring these questions, which inherently required working large spatio-temporal scales. In this Invited View, I discuss current questions that are at the leading edge of this research. I first point out some surprising knowledge gaps in our understanding of pollinators' response to global change. I then outline several ways in which current understanding of the biodiversity-ecosystem functioning relationship might be transformed by studies conducted at large spatio-temporal scales. Specifically, I propose two hypotheses that relate to the number of species required to saturate ecosystem function, and to the mechanisms through which biodiversity stabilizes ecosystem function over space or time.

**Keywords:** Bee; Ecosystem function; Environmental change; Land-use change; Pollinator

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## Zusammenfassung

Die Untersuchung globaler Umweltänderungen und ihrer Wirkungen auf Biodiversität und Ökosystemfunktionen steht an einem hochinteressanten Scheideweg. Hier werden Ideen, die weitgehend durch Theorien und kleinräumige Experimente entwickelt wurden, nun an Ökosystemdiensten wie sie der Bevölkerung in realen Landschaften erbracht werden, getestet. Bestäuber und Bestäubung erweisen sich als ein Modellsystem für die Erforschung dieser Fragen, die inhärent erforderten, mit großen räumlich-zeitlichen Skalen zu arbeiten. In diesem ‘Invited View’ diskutiere ich aktuelle Fragen, die sich an der Spitze dieser Forschungsrichtung stellen. Ich weise zunächst auf einige überraschende Lücken in unserer Kenntnis zu den Reaktionen von Bestäubern auf den globalen Wandel hin. Ich skizziere dann einige Möglichkeiten, wie unser Verständnis der Beziehung zwischen Biodiversität und Ökosystemfunktion durch Studien auf großen räumlich-zeitlichen Skalen verändert werden könnte. Insbesondere schlage ich zwei Hypothesen vor: diese beziehen sich auf die Zahl von Arten, die benötigt werden, um die Ökosystemfunktion abzusättigen, sowie auf die Mechanismen, durch welche die Biodiversität die Ökosystemfunktion in Raum und Zeit stabilisiert.

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We are living in the age of the Anthropocene, a geologic epoch defined by human transformation of the earth (Ellis, 2011). These human transformations are causing a loss of global biodiversity on a scale that has not been experienced since the end of the age of the dinosaurs (Barnosky et al., 2011). Biodiversity itself is an important driver of ecosystem functions and services, such as biomass production and decomposition, which are essential to human welfare (Hooper et al., 2012; Tilman, Reich, & Isbell, 2012). Thus, understanding the relationships among environmental change, biodiversity, and ecosystem function in the real world has not only intellectual interest but also great applied value. Until recently, however, research in this field has proceeded along two largely separate paths (Cardinale et al., 2012). The first path involves theory and small-scale experiments, and has largely driven the field’s conceptual advances. The second involves ecosystem services as they are delivered to people in real landscapes, operates at large spatio-temporal scales at which experiments are difficult, and has been less conceptually driven (Cardinale et al., 2012). As a result of the disconnect between these two lines of research, we lack a conceptual and mechanistic understanding of how ecosystem services operate in real-world ecosystems.

Pollinators and pollination offer a promising model system for testing hypotheses about the relationships among global change, biodiversity and ecosystem services at the landscape scale. Animal-mediated pollination is required by 87% of angiosperm species (Ollerton, Winfree, & Tarrant, 2011), including 75% of crop plants (Klein et al., 2007). Thus, pollinators are essential to ecosystem functioning in natural systems, and also provide important ecosystem services (the subset of ecosystem functions that directly benefit humanity; because pollination is both a function and a service, I use both terms throughout this article). Animal-mediated pollination offers several important advantages as a model system for biodiversity-ecosystem functioning (BEF) research, and it meets all four criteria outlined in a recent review as being most essential to making intellectual progress in this field (Peh & Lewis, 2012). First, pollination necessarily includes

more than one trophic level, whereas most BEF research thus far has focused on a single trophic level. Second, pollination can readily be explored at large spatial scales, whereas most research to date has been at small scales. Third, pollination when studied across landscape gradients can be used to investigate the effects of non-random species loss in response to global change, whereas most previous BEF research has been based on randomly assembled communities. And fourth, pollination is a model system other than those that currently dominate the BEF literature, namely aquatic and temperate grassland communities (Peh & Lewis, 2012). In addition, as a functional group pollinators provide excellent grounds for biodiversity studies, whether these focus on richness, evenness, a diversity index, or some other metric (for the remainder of this article I refer to these broadly as ‘biodiversity’), with often a hundred or more pollinator species present at a single field location.

In this Invited View, I discuss recent research on pollinators and pollination that is rapidly advancing our knowledge of the relationships among global change, biodiversity and ecosystem services at the landscape scale. I do not aim to review what is known about either pollination as an ecosystem service, or the importance of undertaking BEF research at large spatio-temporal scales (‘landscape scales’), because both have been done well elsewhere (Duffy, 2009; Kremen, 2008). Rather, I focus on important questions about pollination in a BEF context that remain unanswered, and on ways in which landscape-scale studies might transform current understanding about the relationship between biodiversity and ecosystem services. Specifically, I propose two hypotheses that relate to the number of species required to saturate ecosystem function, and to the mechanisms through which biodiversity stabilizes ecosystem function over space or time.

## Global change and pollinator biodiversity

In this section, I highlight four important but largely unanswered questions about how pollinator biodiversity is affected by global change. Three of these questions relate to land-use

change, which is the leading cause of biodiversity loss worldwide (Sala, Chapin, Amnesto, Berlow, & Bloomfield, 2000), and also the main form of global change that has been studied thus far for pollinators. One question relates to climate change, which looms large as a future driver of biodiversity loss (Sala et al., 2000).

### How are pollinators affected by moderate land-use change?

It is widely believed that pollinators are in decline due to land-use change (Potts et al., 2010), and recent reviews and meta-analyses suggest that the impacts of human land use on pollinators are, on the whole, negative (Williams et al., 2010; Winfree, Aguilar, Vazquez, LeBuhn, & Aizen, 2009; Winfree, Bartomeus, & Cariveau, 2011). However, it is less appreciated that pollinator response to land-use change has been studied predominantly in dramatically altered systems where, for example, less than 5% of the native vegetation remains in the larger landscape around a study site (Winfree et al., 2009, 2011). If researchers have chosen study systems at the high end of the land-use intensity gradient, this would constitute a research bias which would in turn limit our scope of inference about pollinators in less altered systems. Where human land-use is more moderate, pollinator responses are variable and sometimes positive (Winfree et al., 2009, 2011). Some of the most interesting questions – for example, through which biodiversity stabilizes ecosystem function – are best studied in moderately impacted systems where sufficient biodiversity is still present, and remain relatively unexplored for pollinators.

### What are species-specific responses to land-use change?

The great majority of studies investigating pollinator response to land-use have measured only pollinator abundance and species richness, while few have investigated changes in species composition (Winfree et al., 2011). Thus we have a limited understanding of *which* pollinator species are sensitive to land-use change. Among the bees, with the exception of the genus *Bombus*, and the western European and British fauna (Goulson, Hanley, Darvill, & Ellis, 2006), habitat affinity for most species is poorly known. For example, in eastern North America we know that native bee community composition has shifted dramatically over the past century (Bartomeus et al., 2013), but we do not know which species do well in human-modified habitats, and which do not. These knowledge gaps need to be filled before we can predict how land-use change will affect pollination services (see below).

### Does pollinator body size predict the spatial scale of response to land cover?

Ecosystem services are provided by natural and semi-natural habitats, or by the species that use these habitats. Thus an important question for the management of ecosystem services is, at what spatial scale does land cover most strongly influence ecosystem service delivery? Pollination offers an excellent opportunity to explore this question (Kremen et al., 2007). Bees, which are the most important pollinator taxon in many types of ecosystems (Winfree et al., 2011), are central-place foragers. This ties the pollination services delivered by bees to the land cover in the surrounding landscape. Furthermore, for bees the female's foraging radius around the nest is predicted by body size (Greenleaf, Williams, Winfree, & Kremen, 2007). Thus we expect a larger species to be most strongly affected by landscape-scale land cover and smaller species by more local-scale land cover. The few empirical tests of this idea have provided mixed support, however (Steffan-Dewenter, Münzenberg, Bürger, Thies, & Tschardtke, 2002; Westphal, Steffan-Dewenter, & Tschardtke, 2006; Winfree & Kremen, 2009). A difficulty in separating the relative effects of the different spatial scales on pollination is that land cover tends to be positively auto-correlated across scales, thus making the influence of different scales difficult to separate statistically. When study sites are selected such that land cover at the local and landscape scales are uncorrelated, local-scale land cover is the strongest driver of crop pollination services (Benjamin, Reilly, & Winfree, submitted for publication). Lastly, if pollinator species of different body sizes are affected by land-use at different spatial scales, this could make aggregate pollination services more robust to land-use change than they would otherwise be, through a mechanism known as cross-scale resilience (see below).

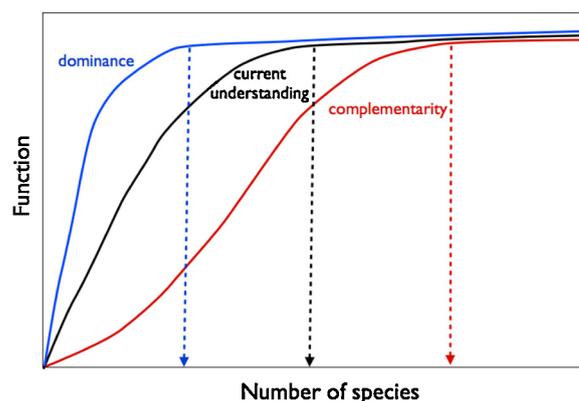
### How will climate change affect the plant-pollinator interaction?

Pollination, like other ecosystem functions that rely on a mutualistic interaction, could be vulnerable to climate change if the plant and animal partners use different environmental cues to time their activity periods. Specifically, plants that bloom before or after their pollinators are active could fail to reproduce, whereas pollinators emerging before or after plant bloom could fail to find food sources. Such phenological mismatching might be particularly likely for early spring species, which respond strongly to climate change rates (Bartomeus et al., 2011). However, the few empirical studies to investigate this issue have found largely congruent phenological shifts for plants and pollinators. An experimental study in the Rocky Mountains, USA suggests that plants and their pollinators use similar environmental cues to time their spring emergence (Forrest & Thomson, 2011). And over a 140-year time period in eastern North America,

spring pollinators and the plant species they visit seem to be advancing their seasonal phenologies at similar rates (Bartomeus et al., 2011). Climate warming could disrupt plant–pollinator interactions in ways not revealed by these broad-scale studies, however. For example, the phenology of interactions between specialist partners might be more readily disrupted, because they lack the insurance provided by having multiple partners which do not all change their phenology in the same way (Bartomeus, Park, Gibbs, Danforth, & Winfree, in press). And because flowering phenologies advance faster at higher latitudes, migratory pollinators that depart from their wintering grounds at the phenologically appropriate time might arrive on their breeding grounds too late in the flowering season (McKinney et al., 2012).

### Pollinator biodiversity and pollination function

In this section, I discuss how the answer to a key question in BEF research – How many species are needed to provide ecosystem function? – might change as research expands to larger spatio-temporal scales. The number of species required to provide a particular ecosystem function can be estimated by plotting aggregate ecosystem function against species richness, and determining the richness level at which function asymptotes or saturates. While other approaches can be used, for simplicity I focus this discussion on richness and saturation. The conclusion from the first generation of BEF experiments was that the level of functioning saturates with a small number of species (Schwartz et al., 2000). Most of this research, however, was conducted at small spatio-temporal scales; for example, the median plot size for experiments using terrestrial plants, which have been the focus of many BEF studies, is 3 m<sup>2</sup> (Cardinale et al., 2011). Recent work suggests that many more species will be found important to function when the spatio-temporal scale of the research increases. For example, within experiments, the relationship between species richness and ecosystem functioning becomes less saturating in longer time series (Reich et al., 2012). And when multiple experiments are combined to increase both the temporal and the spatial scale of the analysis, many more species are revealed to be important to function (Isbell et al., 2011). Another interesting experiment that used combinations of up to five bee species in cages with flowering plants found that although pollination function asymptoted when only a few bee species were present, pollination function was considerably higher in cages left open to the real-world pollinator community. This suggests that the asymptote was an artifact of the small number of pollinators that it is feasible to include in such combinatorial experiments (Fründ, Dormann, Holzschuh, & Tschamtkke, 2013). All of these recent studies, while expanding the spatio-temporal scope of BEF research considerably, are still based on experiments done at small scales and may not be representative of ecosystem service delivery in real landscapes.



**Fig. 1.** The hypothesized effect of adding two factors typical of real-world ecosystems to the current understanding of the BEF relationship. When complementarity across space and time is included, asymptotic function requires more species (red line). When realistic dominance structure is included, asymptotic function is achieved with fewer species (blue line). Although these two effects are portrayed as having similar magnitude for simplicity, in fact it remains to be discovered which of the two is the stronger, and thus what the net effect of them on the BEF relationship is. (For interpretation of the references to color in this figure citation in text, the reader is referred to the web version of this article.)

I propose that the scaling up from experiments to landscapes will change the number of species required for providing a given ecosystem function in two contrasting directions. First, the number of species needed to saturate ecosystem function should *increase* with the spatio-temporal scale examined. This is because the variation in species composition and abundance over space and time should lead to complementarity among species in these dimensions (Duffy, 2009); Fig. 1. For example, the species pollinating a single plant species vary widely across spatial scales of tens of km (Moeller, 2005). And at a single location, the identity of the most functionally important crop pollinators varies between years (Kremen, Williams, & Thorp, 2002). Studies of plant–pollinator networks, while generally not measuring pollination function, also provide support for the idea that the interaction partners of a given species change considerably over time (Alarcon, Waser, & Ollerton, 2008; Petanidou, Kallimanis, Tzanopoulos, Sgardelis, & Pantis, 2008).

Second, the strong numerical dominance typical of ecological communities should *decrease* the number of species important to function. This is because in communities with high dominance, only a few species account for most of the individuals; thus it is likely that those few species account for most of the function as well (Vázquez, Morris, & Jordano, 2005). In contrast to the strong dominance that typifies many natural communities, experimental communities have generally been created to have low dominance, such that all species represented by a similar number of individuals (Hillebrand, Bennett, & Cadotte, 2008); Fig. 1. A recent meta-analysis found that increasing dominance strongly reduced the difference between monocultures and polycultures in terms of

the biomass produced (Zhang, Chen, & Reich, 2012). In other words, adding additional species, if they are only represented by a few individuals, does little to increase ecosystem function. While this point would probably not surprise many ecologists, it has nonetheless not been incorporated into BEF research until rather recently (Hillebrand et al., 2008). Thus overall, I propose that the number of species required for asymptotic function at the landscape scale will depend on the interplay between spatio-temporal complementarity, which should increase the number of species required, and dominance, which should decrease it (Fig. 1).

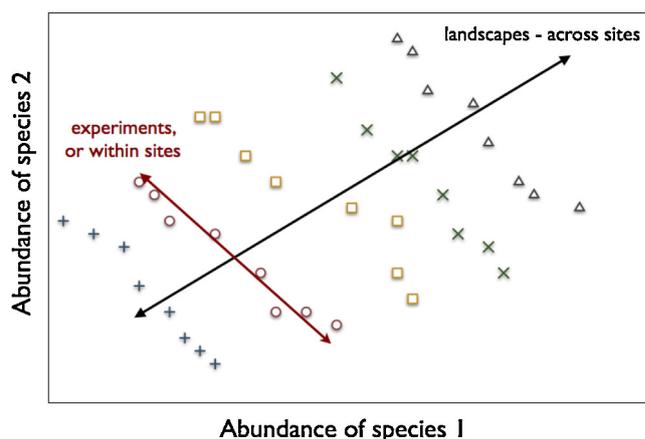
### How does pollinator biodiversity stabilize pollination?

In the remainder of this Invited View, I discuss one of the key unanswered questions in BEF research: What are the mechanisms through which biodiversity stabilizes ecosystem function against global change? Stability in this context is often measured as a ratio, the mean/standard deviation of function, calculated over time (Tilman, Reich, & Knops, 2006). In a landscape context, stability could also be measured over space (Winfree & Kremen, 2009). A positive relationship between biodiversity and the temporal stability of the ecosystem functions has been found empirically in many studies (Cardinale et al., 2012). However, the mechanisms that underlie this relationship are poorly understood (Cardinale et al., 2012). Furthermore, these stabilizing mechanisms have been studied primarily in small-scale, experimental systems (Ives & Carpenter, 2007; Kremen, 2005). Here I propose that different stabilizing mechanisms might be important at the experimental versus the landscape scales.

The three stabilizing mechanisms I consider here are all based on compensatory, or asynchronous, abundance fluctuations among the different species providing the same ecosystem function. They are termed *density compensation*, *response diversity*, and *cross-scale resilience*. Below, I discuss each of these mechanisms in turn, in light of their likely importance in real-world ecosystems. I conclude by outlining what we still need to know about stabilizing mechanisms to predict how ongoing biodiversity loss will impact ecosystem services.

#### Density compensation

The mechanism that has been found most often in experiments is density compensation, or negatively correlated fluctuations in abundance among species over time, and is thought to be caused by competitive release (Tilman, 1999). I propose that experiments may be predisposed to find density compensation because they control resource availability, thus creating a zero-sum game that makes competitive release more likely. In contrast, in real ecosystems



**Fig. 2.** The hypothesized relationship showing negative correlations between species at small scales, but positive correlations at large scales. At small scales, resources vary less, leading to competitive interactions and negatively correlated abundances. At large scales, resources vary more, with some sites being better for all species. Figure after Shea and Chesson (2002), who made a related argument about native and exotic species.

resource availability at a site is likely to vary over time, making density compensation less likely, although still possible (Fig. 2, “experiments, or within sites” arrow). Furthermore, density compensation is even less likely to stabilize ecosystem services against disturbance in real landscapes, because resources typically vary with the disturbance gradient, creating positive rather than negative correlations in abundance among species (Fig. 2, “landscapes, across sites” arrow; note however that this figure assumes no response diversity, as further discussed below). Consistent with this hypothesis, data from real-world ecosystems show little density compensation (Houlahan et al., 2007; Karp, Ziv, Zook, Ehrlich, & Daily, 2011; Winfree & Kremen, 2009). Thus a primary mechanism through which biodiversity stabilizes function in experiments may not exert strong stabilizing effects in real ecosystems.

#### Response diversity

Conversely, a second stabilizing mechanism termed response diversity might exert stronger stabilizing effects in real ecosystems than it has thus far in experiments. Response diversity refers to differential responses to environmental change among species that provide the same ecosystem service (Walker, Kinzig, & Langridge, 1999). Thus, it has the potential to stabilize the aggregate service against environmental change. Broadly, because species have different environmental niches (Amarasekare, 2003), we should expect to observe response diversity. More specifically, the stabilizing effect of species’ differential responses to environmental variation over space or time is not a new idea in ecology. It is a component of the storage effect, through which biodiversity itself is stabilized (Chesson, 2000). (Note

that the storage effect is a very different form of stabilization, however, in which species co-existence is stabilized, whereas within the BEF field a stabilizing mechanism refers to the way in which biodiversity stabilizes ecosystem function.)

Previous research on biodiversity and the stabilization of ecosystem functioning has probably underestimated response diversity because it has been predominantly experimental, and most experiments control environmental conditions, thereby excluding the possibility of response diversity. Experiments that have explicitly looked for response diversity have found it (Leary & Petchey, 2009; Romanuk, Vogt, Young, Tuck, & Carscallen, 2010). Observational studies from real-world systems have likewise found response diversity (Bartomeus et al., 2013; Brittain, Kremen, & Klein, 2013; Cariveau, Williams, Benjamin, & Winfree, 2013; Karp et al., 2011; Rader, Reilly, Bartomeus, & Winfree, 2013; Thibaut, Connolly, & Sweatman, 2012; Winfree & Kremen, 2009). Lastly, because response diversity could occur with respect to many types of environmental disturbances, studies of any one type of disturbance will likely underestimate the true magnitude of response diversity. For example, independent studies of the pollination of the same crop plant found response diversity among bee species in terms of response with respect to land use change (Cariveau et al., 2013), and also with respect to climate warming (Rader et al., 2013), but neither study integrated across disturbance variables to predict the total effect of response diversity. Lastly, response diversity could stabilize the phenological overlap between a plant and its pollinators, if different pollinator species show differential phenological shifts with respect to plant bloom (some pollinators advancing their phenology faster than the plant, others more slowly than the plant) with increasing climate change (Bartomeus, Park, Gibbs, Danforth, & Winfree, *in press*). In sum, response diversity may be the most important mechanism through which biodiversity stabilizes ecosystem services in the real world, yet it has been little investigated.

### Cross-scale resilience

Cross-scale resilience refers to differential responses across species to the same environmental factor across spatial or temporal scales. Thus when cross-scale resilience occurs among the species providing the same ecosystem service, the aggregate service could be stabilized against environmental change (Kremen, 2005; Laliberté et al., 2010; Peterson, Allen, & Holling, 1998). We should expect to find cross-scale resilience because species coexistence is facilitated when species use space as a niche axis (Amarasekare, 2003). The extent to which cross-scale resilience actually stabilizes ecosystem services has been little explored (Winfree & Kremen, 2009). Bee pollinators provide a good model system for exploring the importance of cross-scale resilience at the landscape scale because of their central place foraging, the known relationship between bee body size and foraging radius, and the measurability of the ecosystem service bees provide.

### Stabilizing mechanisms in real landscapes: what do we need to know?

Given the importance of stabilizing ecosystem services against global change, it is surprising that the most basic questions about stabilizing mechanisms have yet to be answered. First, how often do stabilizing mechanisms occur in real-world systems? In order to answer this, we need quantitative tests that would allow us to detect stabilizing mechanisms and, optimally, to separate them from each other. At present there are statistical tests for the existence of density compensation and response diversity (Winfree & Kremen, 2009), although this last test may not serve its purpose well (Cariveau et al., 2013); there is no quantitative test for cross-scale resilience. Second, to what extent are ecosystem services actually stabilized by these stabilizing mechanisms? The answer is poorly known because most field studies do not measure the ecosystem service directly, but instead use a proxy such as the abundance of the service-providing organisms. The sole direct test thus far found that diverse responses to land use change among pollinators stabilized crop pollination substantially, such that the decline in aggregate pollination across a land use gradient would have been up to 62% greater in the absence of the pollinator species robust to land use change (Cariveau et al., 2013). And third, does the stabilization of function provided by each mechanism increase with increasing biodiversity? Oddly, this is the key question that the research on stabilizing mechanisms set out to answer, yet it has scarcely been investigated.

An important area for future research will be to develop study designs and analysis techniques that can separate the contributions to overall stabilization of function by each of density compensation, response diversity and cross-scale resilience. This may not be easy, not only because we currently lack robust quantitative methods for measuring the extent to which each of these mechanisms actually stabilizes function (Cariveau et al., 2013; Winfree & Kremen, 2009), but also because the mechanisms may often co-occur in nature. For example, changed environmental conditions could cause response diversity if two species respond differently to the change, and could simultaneously cause density compensation if the species that was previously the competitive dominant decreases under the new conditions, thereby reducing competitive effects and allowing the second species to increase. Similarly, if species show strong responses to land-use change in general, this makes both response diversity (strong responses that differ in sign and/or magnitude) and cross-scale resilience (strong responses at different scales) more likely.

Lastly, response diversity is closely linked to the idea that the BEF relationship becomes less saturating as the spatio-temporal scale of the analysis increases (see Pollinator biodiversity and pollination function section). For example, consider pollination services delivered to a target plant species at sites that differ in land-use context. Aggregate

pollination services could be similar in magnitude at all sites, but the species providing the pollination could be largely non-overlapping between sites situated in natural versus disturbed landscapes. An analysis that explored species-level changes in function across the land-use gradient would call this response diversity, and conclude that response diversity stabilizes pollination across the land-use gradient. But an analysis that used the same data to calculate the proportion of species important to ecosystem service delivery as a function of the spatial scale considered would conclude that more species are required as the scale of the analysis increases. In both cases, though, the underlying mechanism would be complementarity among the species providing the function; essentially, that different pollinator species occur in different habitats or landscapes. In sum, biodiversity may stabilize ecosystem services in real landscapes for the same underlying reason, albeit via somewhat different mechanisms, as has been found in experiments: complementarity among species in terms of their niches, not only in terms of environmental factors, but also in space and time.

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