



Dispersal and diversity in experimental metacommunities: linking theory and practice

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There has been a recent rise in the number of experiments investigating the effect of dispersal on diversity, with many of the predictions for these tests derived from metacommunity theory. Despite the promise of linking observed relationships between dispersal and diversity to underlying metacommunity processes, empirical studies have faced challenges in providing robust tests of theory. We review experimental studies that have tested how dispersal affects metacommunity diversity to determine why shortcomings emerge, and to provide a framework for empirical tests of theory that capture the processes structuring diversity in natural metacommunities. We first summarize recent experimental work to outline trends in results and to highlight common methods that cause a misalignment between empirical studies and the processes described by theory. We then identify the undesired implications of three widely used experimental methods that homogenize metacommunity structure or species traits, and present alternative methods that have been used to successfully integrate experiments and theory in a biologically relevant way. Finally, we present methodological and theoretical insights from three related ecological fields (coexistence, food web and priority effects theory) that, if integrated into metacommunity experiments, could help isolate the independent and joint effects of local interactions and dispersal on diversity, and reveal the mechanisms underlying observed dispersal–diversity patterns. Together, these methods can provide stronger tests of existing theory and stimulate new theoretical explorations.

Synthesis Although metacommunity experiments offer a unique opportunity to test classic and emerging theory on the relationship between dispersal and diversity, several common challenges have hindered robust tests of theory. We outline how emerging theory on the invasion criterion, food webs and priority effects could help clarify when and how dispersal affects metacommunity diversity, and identify when experimental approaches that homogenize metacommunities fail to test existing theory. By forging better links between theoretical and empirical work, we hope to motivate novel and improved experimental approaches to understanding the joint effects of local and regional processes on diversity.

A central goal in ecology is to understand the processes that maintain biodiversity (Chesson 2000, Hubbell 2001). The growth of metacommunity ecology over the past several decades represents a major advance toward this goal; by describing processes through which local species interactions and dispersal together determine the diversity of species living in spatially structured environments, metacommunity research has helped move ecology beyond the local scale (Levins and Culver 1971, Shmida and Wilson 1985, Holt 1993, Holyoak et al. 2005). These processes have been grouped into four paradigms that form the theoretical framework for metacommunity ecology, and are distinguished by differences in the roles of habitat heterogeneity, competitive asymmetries and dispersal rates in structuring local and regional coexistence (Supplementary material Appendix 1 Table A1; Leibold et al. 2004, Holyoak et al. 2005).

Since this conceptual synthesis of metacommunity ecology (Leibold et al. 2004), theoretical work in this field

has expanded on these classic paradigms to provide a more nuanced understanding of the processes that structure metacommunities. For instance, the growing recognition that aspects of multiple paradigms are likely to characterize any given system has led to calls for research that integrates across paradigms to include multiple metacommunity coexistence mechanisms (Holyoak et al. 2005, Logue et al. 2011, Winegardner et al. 2012). Likewise, recent theory has begun to incorporate links between metacommunity dynamics and ecosystem function (Massol et al. 2011), and to investigate how complex processes such as evolutionary dynamics (Urban et al. 2008, Vanoverbeke et al. 2015) and asymmetric dispersal in dendritic networks (Altermatt 2013) shape metacommunities.

One core focus in metacommunity ecology that has received increased attention in recent years is the relationship between inter-patch dispersal rate and metacommunity diversity (Kneitel and Miller 2003, Cadotte 2006a, Howeth

and Leibold 2010b). As theory describing this relationship has developed (Loreau and Mouquet 1999, Mouquet and Loreau 2003, Altermatt et al. 2011, Pillai et al. 2011, Gilbert 2012, Haegeman and Loreau 2014), there has been a rapid rise in the number of studies using microcosm, mesocosm and field experiments to empirically test the effect of dispersal on diversity at the alpha (within-patch), beta (between-patch) and gamma (metacommunity-wide) scales (Supplementary material Appendix 2 Fig. A2). Together, this growing body of theoretical and experimental work has demonstrated that dispersal strongly shapes coexistence and diversity in metacommunities (Mouquet and Loreau 2003, Cadotte 2006b).

Despite efforts to link observed relationships between dispersal and diversity to underlying processes, experimental investigations have faced unique challenges in creating empirical tests that elucidate the processes that are described by theory and observed in natural metacommunities. This is in part because the homogenization of dispersal rates, starting communities and environmental conditions across patches – which would normally be considered rigorous experimental design – can impede the mechanisms that allow coexistence and shape metacommunity diversity. Likewise, diversity in metacommunities is often shaped by multiple coexistence mechanisms acting at several spatial scales on species with unknown competitive and trophic interactions, which makes a mechanistic interpretation of experimental results difficult. This inherent complexity necessitates creative methods and novel approaches to help untangle how and why dispersal impacts metacommunity diversity.

Here we provide a review of metacommunity experiments that investigate the relationship between dispersal and diversity in order to highlight ways in which experimental approaches could be improved to provide more robust tests of theory. We clarify how three commonly-used experimental methods prevent tests of metacommunity processes by eliminating interspecific and inter-patch differences, and highlight alternative but under-utilised methods that researchers have developed to overcome these issues. We then review techniques and insights emerging from related ecological fields (coexistence, food web and priority effects theory) that could facilitate a more mechanistic understanding of the relationship between dispersal and diversity. Despite the challenges facing metacommunity empiricists, thoughtful experimental approaches that incorporate heterogeneity and integrate emerging theory promise to untangle complex processes and strengthen the link between theory and empirical work in this rapidly growing field.

Data deposition

A table of all included studies is available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.nq853>> (Grainger and Gilbert 2016).

20 years of experimental metacommunities

Search methods

We conducted a review of published experiments testing the relationship between dispersal and diversity in metacommunities, and summarized the results obtained (Fig. 1) and the methods used (Fig. 2) by these studies. We

included experiments that manipulated either the rate at which individuals move between habitat patches or the connectivity of patches, and measured the resulting effect on species diversity at the local (alpha or α), inter-patch (beta or β) or regional (gamma or γ) scales (see Supplementary material Appendix 2 for detailed search methods and inclusion criteria). We included multispecies (≥ 3) studies that had two or more levels of dispersal (including any no-dispersal controls). We excluded seed rain and species addition experiments where colonists came from an external species pool and no information on species establishment post-colonization was provided. We also excluded fragmentation studies that only compared diversity in fragments to diversity in continuous habitat, and experiments focused solely on the effect of dispersal on recovery after severe disturbance. Fifty studies met our criteria and were included; all of these studies were published within the last twenty years, and 24 were published within the last five years. These experiments ranged from highly controlled lab experiments that used artificial species assemblages, to semi-natural outdoor mesocosms, to field experiments conducted in situ in grasslands, bromeliads, pitcher plants or moss patches.

Summary of experimental hypotheses and results

Although a variety of organisms and experimental methods were used in these studies, the stated hypothesis for the effect of dispersal on local (alpha) diversity was fairly consistent across studies. Most authors hypothesized a hump-shaped relationship between dispersal and alpha diversity, as predicted by a commonly-cited model of source-sink metacommunities (Mouquet and Loreau 2003). However, only six of the 30 studies that quantified alpha diversity across three or more dispersal treatments actually detected a hump-shaped relationship (Fig. 1). This may be in part

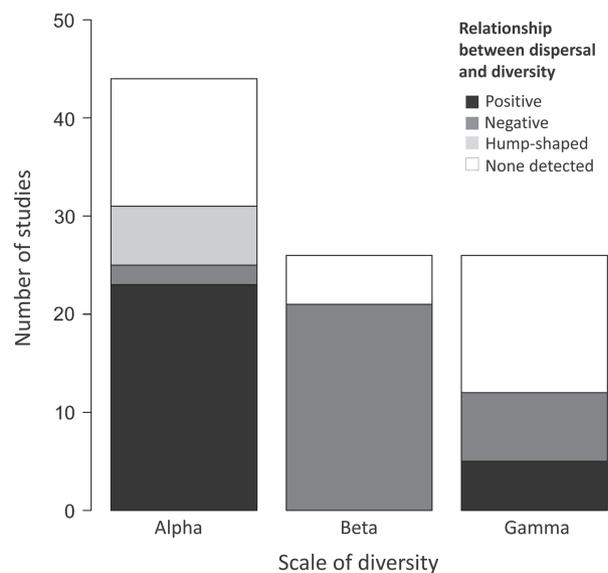


Figure 1. Summary of results reported by experimental studies included in our literature review. Bars indicate the effect of increasing dispersal on local (alpha) richness, between-patch similarity (beta diversity) and regional (gamma) richness. See Grainger and Gilbert (2016) for a full list of included experiment and their corresponding results.

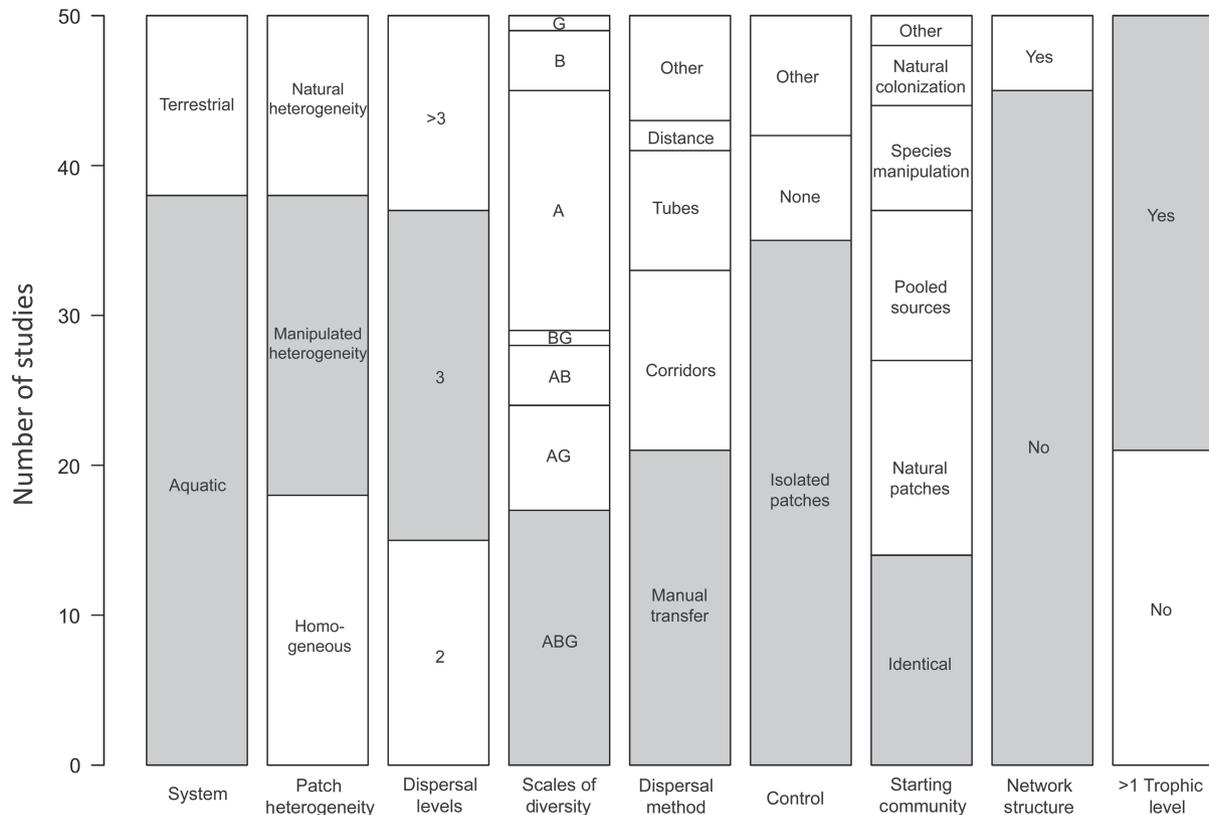


Figure 2. Summary of methods used in experimental studies included in our literature review. The most commonly used method is highlighted in grey. Patch heterogeneity: manipulated heterogeneity = the experiment included some type of controlled inter-patch heterogeneity (e.g. disturbance, nutrients); homogenous = all patches had the same environmental conditions; natural variation = experiment used natural patches that presumably differed in some environmental conditions. Dispersal levels: the number of levels of dispersal (e.g. low dispersal, high dispersal) included in the experiment, including any no-dispersal controls. Scales of diversity: the diversity metrics that were reported. A = alpha; B = beta; G = gamma (see Supplementary material Appendix 2 for details). Dispersal methods: manual transfer = transferred water containing aquatic organisms between patches or transferred organisms between patches; corridors = terrestrial habitat connecting patches; tubes = tubes connecting patches through which aquatic organisms can pass; distance = manipulated inter-patch distances and allowed organisms to move freely between patches. Control: type of control used for dispersal treatment (e.g. isolated patches with no dispersal). Starting communities: identical starting communities = all patches started with the same suite of species; natural patches = the species assemblage of each patch was (or was sourced from) a patch in a natural metacommunity; species manipulation = each patch was seeded with a different suite of species; natural colonization = patches were left open to be colonized. Network structure: whether or not experiments tested for effects of network structure or directional dispersal. Trophic level: whether or not diversity results included species from more than one trophic level. See Grainger and Gilbert (2016) for a full list of included experiments and their corresponding results.

because the assumptions of Mouquet and Loreau's (2003) model (e.g. heterogeneous patches, one trophic level) were not met by most studies, and altering competitive dynamics or adding trophic interactions can have important implications for the dispersal–diversity relationship (Gilbert 2012, Haegeman and Loreau 2014). In particular, certain experimental choices may be more likely to produce this relationship; all six studies that detected a unimodal relationship did so under conditions with no predators, and with each patch initially containing a different local community (Kneitel and Miller 2003, Matthiessen and Hillebrand 2006, Howeth and Leibold 2010b, Matthiessen et al. 2010b, Severin et al. 2013). The implications of these and other experimental methods on the dispersal–diversity relationship are described in the sections below.

Gamma diversity likewise exhibited a variety of relationships with dispersal, including positive, negative and no effect (Fig. 1); however these results showed no consistent

association with the experimental methods used. The relationship between dispersal and beta diversity was consistently negative, as predicted if dispersal between patches facilitates the homogenization of local communities (Fig. 1).

Summary of experimental methods

The variety of relationships between dispersal and alpha and gamma diversity detected in metacommunity studies suggests that there may be underlying differences in the systems studied or the methods used. Indeed, our review of the methods employed by these studies revealed that while some methods were highly consistent across studies, others varied markedly. We focus on methods that may have undesired implications for understanding the mechanisms underlying dispersal–diversity relationships (Fig. 2). As in previous discussions of this topic (Cadotte 2006b, Logue et al. 2011), we noted the prevalence of the following experimental choices that impact how closely experiments match

natural metacommunities and/or theory: a strong preference for using aquatic microcosms and mesocosms (70% of studies); precluding mass effects and species sorting by using homogeneous patches (36% of studies); precluding the detection of hump-shaped responses by including only two levels of dispersal (30% of studies); and failing to report all levels of diversity (α , β , γ) despite requiring all measures to distinguish underlying mechanisms that structure diversity (66% of studies) (Fig. 2). We do not focus on these shortcomings, as they have been well-described elsewhere (Holyoak et al. 2005, Cadotte 2006a, Logue et al. 2011).

An additional, and underappreciated, concern for metacommunity research arises from the common application of experimental methods that are inappropriate for detecting or even allowing metacommunity processes that drive the dispersal–diversity relationship. In particular, metacommunity diversity can be structured and maintained by heterogeneity at a number of organisational levels including interspecific differences in dispersal ability, heterogeneity in local interactions that arises from only a subset of species being present at each patch, and differences in colonization rates between patches caused by directional dispersal. Although these sources of heterogeneity have been shown to be important in structuring metacommunity diversity in both theoretical work and natural metacommunities, common experimental methods eliminate them. Below, we outline the challenge of incorporating these aspects of metacommunity heterogeneity and highlight research that has advanced the field by finding creative ways to incorporate them.

Incorporating metacommunity heterogeneity

Inter-specific differences in dispersal

Differences in dispersal ability among species can permit coexistence in patchy environments through mechanisms such as a competition–colonization tradeoff or the stabilization of trophic dynamics (Taylor 1990, Tilman 1994). Such interspecific dispersal differences result from different dispersal modes (active, passive and differences in vectors), dispersal abilities, or methods of habitat selection. These differences are an important feature of natural metacommunities (De Bie et al. 2012, Jones et al. 2015) that can have major effects on local and regional coexistence and diversity (Amarasekare 2010, Resetarits and Silberbush 2016). However, the most common method of manipulating dispersal (used by 42% of the studies reviewed here) eliminates these differences; researcher-mediated bulk dispersal involves the transfer of part of a community among patches, for example a volume of water containing a portion of the community in aquatic studies (Fig. 2). Although bulk dispersal increases tractability, it allows only species abundances to generate interspecific differences in dispersal within each dispersal treatment. This homogenization precludes any metacommunity coexistence mechanism that relies on interspecific differences in dispersal. Additionally, while bulk dispersal may mimic a specific type of inter-patch dispersal in aquatic ecosystems resulting from splashing (Kneitel and Miller 2003), it is likely a poor proxy for total dispersal for organisms that disperse actively, are carried passively by wind, or move via hydrological connections (Vanschoenwinkel et al.

2008, Altermatt and Ebert 2010, Pellowe-Wagstaff and Simonis 2014).

While some studies have acknowledged the shortcomings of homogenizing dispersal among species (Matthiessen et al. 2010a, Carrara et al. 2012), others have gone even further to preserve individual species' differences in dispersal. These latter studies have used treatments that alter dispersal by varying either inter-patch distance (Chase et al. 2010), the presence or length of inter-patch connection tubes (Cadotte 2006b, Davies et al. 2009) or corridors (Gonzalez et al. 1998), or the frequency of propagule rains (Matthiessen and Hillebrand 2006, Matthiessen et al. 2010b) (Fig. 2). These treatments promote more natural dispersal among patches and increase experimental realism and adherence to common theoretical assumptions; as a result, these approaches provide some of the best tests of the effect of dispersal on diversity. For example, one study that allowed semi-natural dispersal among patches demonstrated that while only the strongest disperser was able to colonize patches in low dispersal treatments, resulting in low diversity, weaker dispersers dominated the metacommunity in high dispersal treatments (Matthiessen and Hillebrand 2006).

Another common but extreme treatment that removes the advantage of superior dispersers is a completely isolated 'control' treatment (Fig. 2). While several studies have appropriately used this type of treatment to test for rescue effects (Gonzalez et al. 1998, Chisholm et al. 2011), this control can be problematic for researchers attempting to understand the effect of dispersal on diversity via spatial coexistence mechanisms such as a competition–colonization tradeoff, or to predict how dispersal influences the relative abundance of species regionally. In these cases, theory predicts the performance of good dispersers increases as metacommunity connectivity decreases, but that this advantage disappears completely when local communities become totally isolated. Thus, going from very low connectivity to an isolated control with zero connectivity reverses expectations for the relative success of good dispersers. In such cases an isolated control is effectively the opposite treatment of very low connectivity, rather than the next most isolated treatment. Although isolated controls serve a valuable purpose for certain experimental questions, such as clarifying competitive or consumptive dynamics in the absence of dispersal (Shurin 2001), researchers should interpret results from no-dispersal controls carefully and within the context of theory.

Heterogeneous starting communities

Underlying three of the most common hypotheses for dispersal–diversity studies is the assumption that patches within a metacommunity vary in the identity of their constituent species. When dispersal limitation prevents species from colonizing suitable habitat, increasing dispersal has a positive effect on alpha diversity (Gonzalez et al. 1998). Similarly, a decline in diversity at very high dispersal rates can result from a dominant competitor or predator reaching all sites, or from increased synchrony (Taylor 1990, Mouquet and Loreau 2003, Gilbert 2012). Finally, beta diversity is predicted to decline as dispersal increases because local communities become more similar in species composition as species reach all patches. Intuitively and mechanistically, it is evident from these hypotheses that an experiment that

starts each patch with an identical local suite of species will produce vastly different results from an experiment in which patches differ in their initial species composition.

Although the impact that starting community composition may have on the likelihood of experimental outcomes adhering to theoretical predictions is rarely discussed, it is noteworthy that all six of the studies that found a hump-shape relationship between dispersal and alpha diversity used patches that started with different communities (Fig. 1; Kneitel and Miller (2003), Cadotte (2006b), Matthiessen and Hillebrand (2006), Howeth and Leibold (2010b), Matthiessen et al. (2010b), Severin et al. (2013)). Indeed, the impact of starting communities on experimental outcomes was explored empirically by Cadotte (2006b); by creating metacommunities that differed in whether patches initially had identical or different species composition, he demonstrated that a hump-shaped relationship between dispersal and local diversity was only found in metacommunities that had different starting communities. However, despite the apparent importance of varying composition among patches at the outset of experiments, 28% of the studies reviewed here used identical starting communities in each patch (Fig. 2). Of the studies that used different communities, 27 used initial starting communities that were created from a natural community in some way (patches were composed of species drawn from natural patches, pooled sources or natural colonization) and presumably had unquantified inter-patch differences in species composition. Only seven studies used intentionally different starting communities by systematically varying species composition in each patch. Such studies highlight the advantage of this method. For example, Matthiessen and Hillebrand (2006) found that final local diversity could be predicted by which species were initially present in a local assemblage because certain species had facilitative or inhibitory effects on subsequent colonizers. Likewise, France and Duffy (2006) demonstrated that systematically varying starting inter-patch species composition can allow extinctions and colonization to be tracked directly, providing a clear understanding of how dispersal alters alpha, beta and gamma diversity through temporal turnover.

As the initial degree of difference in community composition between patches in an experimental metacommunity can alter experimental outcomes, a clearer justification for using patches with identical starting communities should be included by those researchers who choose this method. Better still, systematically varying starting patch composition, or even quantifying initial inter-patch differences in species composition when patches are seeded from natural sources, would allow researchers to determine how local colonization and extinctions are driving changes in diversity, and provide a more direct link between theory and empirical measures.

Spatial network configuration and directional dispersal

In many natural metacommunities, dispersal follows paths constrained by landscape elements, which results in asymmetric or directional movement of individuals between local sites. Dendritic or riverine networks, where hydrological connections and topography shape dispersal, are one of the most widespread examples of this phenomenon (Benda et al. 2004). A growing body of theoretical and observational

work suggests that the directional, hierarchical and branching nature of such systems, and the resulting asymmetry in colonization rates at local habitat patches, can strongly influence metacommunity diversity (Muneepeerakul et al. 2007, 2008, Brown and Swan 2010, Salomon et al. 2010). For example, theory predicts that inter-patch differences in species composition and abundance that keep beta diversity high are more likely in riverine networks compared to conventional lattice networks (Muneepeerakul et al. 2007, Carrara et al. 2012). Likewise, models have shown that asymmetrical dispersal can result in higher extinction rates (Vuilleumier and Possingham 2006), that can cause declines in local diversity (Muneepeerakul et al. 2007).

Despite mounting evidence of the importance of dispersal asymmetry and network type for the dispersal–diversity relationship, few experimental studies have included dendritic or hierarchical network structure when testing the relationship between dispersal and metacommunity diversity (5 of the 50 studies reviewed here – Fig. 2). However, those that have used dispersal treatments that mimic riverine networks have demonstrated that dendritic connectivity can result in lower local diversity and higher beta diversity (Altermatt et al. 2011, Carrara et al. 2012), and that local diversity may vary predictably with a patch's position within the network (e.g. central versus peripheral, headwater versus confluences) (Carrara et al. 2012, 2014). These early results indicate that incorporating heterogeneity in network structure into metacommunity experiments may be a critical future direction for this field. Indeed, incorporating different network structures would not only test emerging theory, but would also create experiments that better reflect the wide variety of dispersal mechanisms prevalent in natural metacommunities.

Integrating approaches from related fields

Determining which metacommunity processes are driving experimental outcomes presents a formidable challenge to researchers due to the multitude of interacting processes occurring at multiple spatial scales in most experimental systems. Here we outline three bodies of theory developed in related ecological fields that could help disentangle the mechanisms underlying observed dispersal–diversity relationships.

Scaling from local interactions to regional dynamics: the invasion criterion

Metacommunity models generate distinct predictions for the dispersal–diversity relationship that arise from differences in local interactions and how they ‘scale up’ to determine both local co-occurrence and regional coexistence. For example, a competition–colonization tradeoff requires a competitive hierarchy that is consistent across patches (Tilman 1994). In contrast, source–sink dynamics require species to have negative growth rates caused by abiotic conditions or biotic interactions in some patches, and positive growth rates in other patches (Pulliam 1988).

Recent advances in coexistence theory provide a clear method for assessing the outcome of local processes within patches, and could thus be used to decouple the effects of local interactions from regional processes (Chesson 2000,

Adler et al. 2007). Specifically, the invasion criterion is a simple test of species interactions that determines whether local coexistence is possible in the absence of dispersal by assessing whether a species has positive population growth rates when it is at low abundance and its competitors are at equilibrium (Siepielski and McPeck 2010). Mutual invasibility, where all species meet the invasion criterion, is necessary for competing species to stably coexist within a patch in the absence of immigration (Chesson 2000, Siepielski and McPeck 2010). In this framework, coexistence is differentiated from co-occurrence, in which species are slowly declining to extinction or are maintained by incoming colonists (Siepielski and McPeck 2010). Importantly, the invasion criterion allows researchers to determine the patches and species that a focal species can occur in or with, and by inference, when dispersal alters the outcomes of these local processes. While a number of studies have used the invasion criterion to formally evaluate local coexistence in the absence of dispersal (Wilson et al. 1999, Stomp et al. 2004, Jiang and Morin 2007, Godoy and Levine 2014), this method has yet to be integrated into metacommunity ecology.

The invasion criterion is particularly relevant for testing metacommunity dynamics because different metacommunity paradigms make distinct predictions about the maintenance of local diversity in the absence of dispersal. For example, local (within-patch) tests of competitive dominance can be compared among patches to determine whether there is a competitive hierarchy that is consistent across patches; if pairwise tests of the invasion criterion reveal a consistent competitive hierarchy among patches, the local conditions required for a competition–colonization tradeoff are met. Conversely, if competitive hierarchies differ among patches and respond to patch characteristics, species sorting or mass effects are more likely to be driving diversity patterns. In cases where the order of arrival determines the outcome of competition through priority effects, the invasion criterion can be used to identify the alternate stable states that result (Peay et al. 2012). Such tests can also help researchers move beyond testing single paradigms for entire metacommuni-

ties by elucidating species-specific interactions. For example, tests of the invasion criterion can identify when co-occurring species are competitors versus mutualists, which in turn can explain why species show positively or negatively correlated responses to changes in connectivity, and could help to reveal underlying drivers of the dispersal–diversity relationship (Gilbert and O’Connor 2013).

To illustrate how the invasion criterion can distinguish among metacommunity processes, we consider a competitive metacommunity with heterogeneous patches (Fig. 3). In a heterogeneous metacommunity, increasing connectivity could increase alpha diversity either by allowing species to reach preferred patches (species sorting; middle of Fig. 3) or by allowing species to subsidize populations in sub-optimal patches with immigrants from optimal patches (mass effects; right side of Fig. 3). Quantifying the invasion criterion within patches would determine which of these processes is maintaining diversity. In this example, the invasion criterion allows for a clear determination of whether species are persisting in optimal patches or are maintained by immigration from source populations (Fig. 3). Although such tests may appear difficult for large numbers of species, recent work by Levine and colleagues has demonstrated that invasibility tests of multiple species can be undertaken simultaneously within a community when species at very low abundances are only likely to interact with abundant species rather than each other, which greatly reduces the number of experimental treatments required (Levine and HilleRisLambers 2009, Godoy and Levine 2014).

In addition to helping determine which paradigms best describe local processes in a metacommunity, tests of the invasion criterion could allow a researcher to partition the relative influence of each mechanism. For example, theory predicts that local diversity will be low when connectivity is insufficient to get all species to all appropriate patches, and high when connectivity is sufficient for mass effects to subsidize local diversity (Mouquet and Loreau 2003). By determining the proportion of species that are maintained by mass effects or species sorting using the invasion criterion

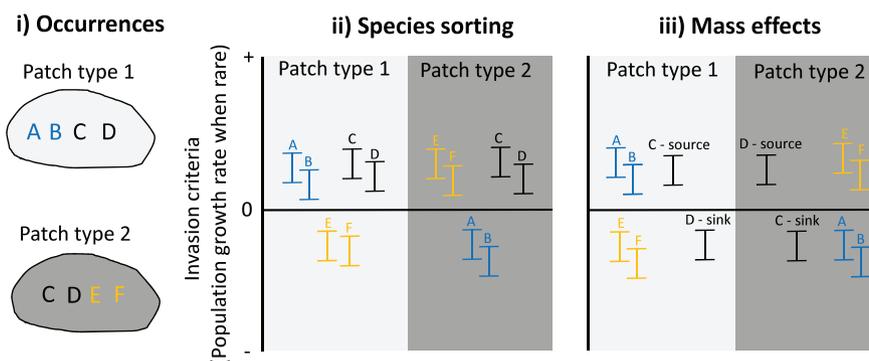


Figure 3. Hypothetical results for an experiment using the invasion criterion to distinguish between species sorting and mass effects in a heterogeneous metacommunity. i) Species A and B are found only in habitat (patch type) 1, species C and D are found in both patch types and species E and F are found only in habitat 2. ii) If species sorting is driving occurrences, all species will be able to invade all patches in which they are found (i.e. population growth rate of each species when rare will be positive in the absence of immigration). iii) If mass effects increase local diversity, species that occur in both patch types (species D and C) will each only meet the invasion criterion in one (source) environment and fail to meet the invasion criterion in the other (sink) environment. Note that the rates of population decline in sink patches must be smaller than immigration rates to maintain these sink populations. In this example, other species (A, B, E, F) are still found in their optimal environments.

methods described in Fig. 3, the relative role of each process could be quantified at any level of dispersal. Similarly, the invasion criterion can determine how frequently species are absent from patches where they could invade, as is predicted to occur when dispersal limitation is shaping species distributions. This type of partitioning approach that facilitates the integration of multiple metacommunity processes could move metacommunity studies into a clearer, more mechanistic understanding of the link between dispersal and diversity.

From competitive metacommunities to food webs: incorporating multiple trophic levels

Although much of metacommunity theory focuses on competitive interactions (Leibold et al. 2004), it is widely recognized that trophic interactions can play an important role in structuring diversity in patchy systems (Gouhier et al. 2010, Pillai et al. 2010, Haegeman and Loreau 2014). However, food webs are inherently complex – even simple webs often consist of several modules, or small groups of species that differ in the nature of their interactions (Holt 1997, McCann et al. 1998). When this complexity is coupled with differential dispersal among species, a broad suite of resulting effects is possible, which has made a general framework for food web metacommunities elusive. Despite this gap, 58% of the experiments reviewed here nonetheless used metacommunities with multiple trophic levels (Fig. 2). Several such studies have assessed the effect of trophic interactions on the dispersal–diversity relationship by including predators as a treatment (Shurin 2001, Kneitel and Miller 2003, Cadotte et al. 2006, Howeth and Leibold 2010a) or as a form of patch heterogeneity (Howeth and Leibold 2010b). Such experiments have demonstrated that trophic interactions can fundamentally alter dispersal–diversity relationships. For example, predation pressure that extirpates species locally can lead to a dampening of the predicted hump-shaped relationship between dispersal and local diversity (Kneitel and Miller 2003, Howeth and Leibold 2010b), which may explain why all six studies that reported a hump-shape found this result under no-predation conditions (Kneitel and Miller 2003, Matthiessen and Hillebrand 2006, Howeth and Leibold 2010b, Matthiessen et al. 2010b, Severin et al. 2013). These findings highlight the necessity of incorporating trophic complexity into metacommunity studies in order to fully understand the dispersal–diversity relationship. Fortunately, recent theory that integrates trophic interactions and metacommunity processes suggests several considerations that could guide empirical research, three of which we discuss here: isolating the effects of local interactions through food web modules, allowing prey and predator dispersal to vary independently, and quantifying how dispersal alters food web metrics (Rooney et al. 2006, Amarasekare 2008, Pillai et al. 2011, Rip and McCann 2011, Haegeman and Loreau 2014, LeCraw et al. 2014).

As with the use of the invasion criterion to determine how dispersal alters local competitive dynamics, local tests of food web dynamics can be used to elucidate mechanisms through which dispersal affects the outcome of local trophic interactions. Locally, the removal of specific species to quantify interaction strengths and stability has been used to clarify trophic interactions within food web mod-

ules (Paine 1992, Gilbert et al. 2014). When these tests are performed in the presence and absence of dispersal, they allow ecologists to quantify exactly how local interactions are modified by dispersal, providing a clear link between theory and experimentation (Rip and McCann 2011). For example, when a predator drives the local extinction of a prey species that would persist in its absence, changes in this outcome when local patches are connected by dispersal would provide evidence of dispersal generating refugia for prey (Taylor 1990). Similarly, when a top predator stabilizes local dynamics by moving between patches, local communities will show less temporal variation as predator dispersal increases (Rooney et al. 2006). Although this approach of decoupling local trophic interactions from regional processes has yet to be adopted in metacommunity studies, many natural mesocosms have had their food webs characterized in previous research and are well suited to such tests (Srivastava et al. 2004). From the perspective of generating a broader framework for food web metacommunities, such separation of local interactions and dispersal could both inform the assumptions of theoretical models and test their predictions.

Understanding the effects of dispersal on even well-understood local food webs requires that dispersal differences among trophic levels be acknowledged and incorporated into theoretical and experimental work. The spatial and temporal scale at which organisms disperse can vary substantially by trophic level, and theoretical work has demonstrated that altering which trophic levels are allowed to disperse can dramatically alter impacts on metacommunity diversity (Shurin and Allen 2001, Amarasekare 2008, Haegeman and Loreau 2014). For example, simulations demonstrated that although a hump-shaped relationship between dispersal and local diversity is predicted when consumer and resource dispersal vary simultaneously, increasing consumer dispersal while keeping resource dispersal low leads to a positive relationship between dispersal and diversity (Haegeman and Loreau 2014). In contrast, theoretical work that examines locally unstable predator–prey dynamics predicts that high predator dispersal can cause both species to go regionally extinct (Taylor 1990). When coupled with tests designed to clarify local interactions, the experimental separation of predator and prey dispersal to determine how dispersal of each trophic level affects diversity could greatly benefit studies of trophic metacommunities (Limberger and Wickham 2011). However, studies that integrate multiple trophic levels often impose dispersal treatments that homogenize dispersal rates across trophic levels (Verreydt et al. 2012, Declerck et al. 2013) or use predation as a treatment to assess how prey diversity varies with dispersal and predation (Kneitel and Miller 2003, Cadotte et al. 2006, Howeth and Leibold 2010a). Methods that allow predators and prey to disperse at more natural, and often vastly different, rates (Gilbert et al. 1998, Chase et al. 2010), or experimentally separate predator and prey dispersal (Limberger and Wickham 2011), provide a better match to natural systems and have great promise for testing and inspiring theory.

In complex food webs where simple modules are insufficient to describe the impacts of dispersal on trophic interactions, measures like stability (e.g. time to extinction) and complexity (e.g. chain length) can help characterize

how food web structure is altered by dispersal (Amarasekare 2008, LeCraw et al. 2014). For example, food webs are predicted to be most stable at intermediate dispersal rates if low dispersal allows asynchrony between patches and enables depleted prey populations to be rescued from extinction and very high dispersal allows prey overexploitation by removing prey refugia (LeCraw et al. 2014). Likewise, chain length is predicted to increase at intermediate dispersal as lower trophic levels are able to get to more patches and build up food chains; however, at very high dispersal, complexity may be reduced if predators drive prey extinct in many patches and lead to their own extinction (reduced chain length) or specialist species can reach every patch and outcompete generalists (decreased chain branching) (Pillai et al. 2011, LeCraw et al. 2014). While there is a substantial body of work outlining theory that links spatial structure to food web properties (Holt and Hoopes 2005, Gravel et al. 2011) and testing it empirically (Huffaker 1958, Holyoak 2000, Bonsall et al. 2002, Vasseur and Fox 2009), these metrics have rarely been integrated into empirical investigations of dispersal–diversity relationships (but see Howeth and Leibold 2010b, Staddon et al. 2010). Complementing species diversity metrics with an assessment of how dispersal alters food web stability and/or complexity could provide valuable mechanistic insights into why and how diversity is affected by dispersal.

Using theoretical insights to inform experimental treatments (e.g. dispersal treatments that allow predators and prey to disperse separately) and responses (e.g. key food web properties) would enhance the realism of these experiments, make them stronger tests of existing theory, and may uncover emergent properties of metacommunities that as of yet remain unknown. Indeed, one of the challenges with the general framework for competitive metacommunities proposed by Leibold et al. (2004) is that it may oversimplify the dynamics in any given metacommunity; deconstructing trophic metacommunities from basic principles could provide the flexibility for researchers to more clearly link theory to empirical data generated from study systems characterized by a variety of competitive and consumptive interactions. Although such complexity makes simple predictions for the effects of dispersal on diversity difficult, the suggested approaches provide a strong foundation for understanding trophically structured metacommunities.

The legacy of colonization history: priority effects

Priority effects are broadly defined as any change in the trajectory of community assembly that results from a change in the order in which species arrive at a local site. For example, priority effects can occur if early arrivers draw down a common resource or modify the environment in a way that prevents subsequent colonizers from establishing (Sutherland 1974, Fukami 2015). Likewise, for species with fast generation times or systems with infrequent dispersal, local adaptation of a species before its competitor arrives may increase the likelihood of the late arriver being excluded (Urban and De Meester 2009). Although the mechanisms through which priority effects alter local diversity have been well-described, their impact on metacommunity diversity remains a subject of active debate (Fukami 2015). In some cases, priority effects in metacommunities may cause positive feedbacks in which the local success of an early colonist hinders late arrivers and leads to the regional domination of that species in the metacommunity (Shurin et al. 2004, Fukami 2015, Vanoverbeke et al. 2015). In other cases, high regional diversity may be maintained in spite of priority effects if abiotic heterogeneity creates spatial refuges (Shurin et al. 2004), or variation in species interaction strength among local communities produces alternative community states (Pu and Jiang 2015). In either case, priority effects can be important determinants of metacommunity diversity. However, the importance of colonization history is only just beginning to be considered in metacommunity experiments (Pu and Jiang 2015, Vanoverbeke et al. 2015).

In metacommunities, species-specific dispersal rates influence the order in which individuals arrive at a local patch, and, through priority effects, this order of arrival can alter coexistence and diversity. The relationship between dispersal rates and priority effects is therefore a potentially important, but largely unexplored, mechanism through which dispersal can alter metacommunity diversity. Recent work on priority effects has made progress in determining when dispersal and local conditions are likely to result in priority effects (Table 1). Three insights from this work could provide new pathways for incorporating priority effects into dispersal–diversity research and offer exciting future directions for metacommunity ecology.

Table 1. The impact of experimental conditions on the likelihood of priority effects.

Attribute	Condition that favors priority effects	References
Dispersal rates	low dispersal rates	Chase 2003 [†] , Fukami 2005 [†] , Kardol et al. 2013 [*] , Fukami 2015 [†] , Vanoverbeke et al. 2015 [†]
Species traits	species' dispersal rates are similar	Fukami 2015 [†]
	species pairs are close relatives	Peay et al. 2012 [*] , Tan et al. 2012 [*]
	species pairs have high niche overlap	Vannette and Fukami 2014 [*]
	species have rapid growth rates	Fukami 2015 [†]
	species strongly impact the environment	Vannette and Fukami 2014 [*]
Local conditions	species can evolve rapidly	Loeuille and Leibold 2008 [†] , Urban and De Meester 2009 [*] , Vanoverbeke et al. 2015 [*]
	productive environment	Chase 2010 [*] , Kardol et al. 2013 [*] , Vannette and Fukami 2014 [*]
	no predators	Chase et al. 2009 [*]
	small habitat size	Fukami 2004 [*]

^{*}experiment, [†]model, [‡]review.

Theory on priority effects predicts that lower dispersal rates should increase the importance of colonization history, because longer time lags between species' arrivals allow early arrivers more time to establish, grow, alter the environment, and evolve (Table 1; Chase 2003, Fukami 2015). This hypothesis is only beginning to be tested empirically, and early experimental evidence is conflicting; while one recent study found that differences in colonization history in a protist microcosm produced alternate community states regardless of dispersal rate (Pu and Jiang 2015), an experiment that manipulated planting intervals in an old field system detected stronger priority effects at longer time intervals (Kardol et al. 2013). If lower dispersal rates can indeed increase the likelihood of competitive exclusion through priority effects, the resulting alternate stable or transient states in local communities could strongly influence alpha, beta and gamma diversity in dispersal–diversity studies. Researchers therefore need to be cognisant of whether priority effects may be occurring within their experimental systems in order to fully capture the spatial scaling of diversity.

Priority effects are also most likely to occur when species have similar dispersal rates, but individuals can arrive at local sites at different times (Fukami 2015). In metacommunity experiments, the method used to manipulate dispersal and the nature of starting communities together determine whether interspecific differences in arrival time, and thus priority effects, can occur. For example, bulk dispersal, in which species arrive at a patch together at each transfer event, eliminates much of the interspecific variation in arrival times that would occur in a natural metacommunity. Likewise, if all species are present in all patches at the start of an experiment, there can be no differences in arrival time and thus no priority effects. Researchers that start with homogenous communities or use methods that synchronize arrival times should consider the implications of eliminating priority effects, while those using methods that allow species to arrive sequentially should consider how priority effects might impact results (Cadotte 2006b, Berga et al. 2015).

Finally, experimental conditions that result in high niche overlap between competitors, or allow early arrivers to rapidly monopolize a patch, are most likely to result in priority effects (Table 1; Peay et al. 2012, Vannette and Fukami 2014, Fukami 2015). This includes systems that contain closely related species with fast growth rates living in small, productive habitats (Table 1). For example, Peay and colleagues used tests of the invasion criterion in nectar yeasts to demonstrate that priority effects were strongest between close relatives (Peay et al. 2012). Notably, many of the conditions and species traits that promote priority effects match the characteristics of systems frequently used in experimental tests of the impact of dispersal on metacommunities. These insights on local conditions that promote priority effects could be used not only to help researchers determine when priority effects are more or less likely to occur in metacommunity experiments, but could also provide clear hypotheses that may be best tested within a metacommunity framework. A continued integration of metacommunity and priority effects research could provide new advances to both

fields, and may be essential to fully understand how dispersal affects metacommunity diversity.

Conclusion

Empirical metacommunity studies have the potential to provide a mechanistic understanding of the effect of dispersal on diversity by clarifying how and when dispersal alters or reinforces local community dynamics. Our review illustrates how experimental methods that preserve heterogeneity in dispersal and community composition have led to novel insights, and can continue to create better experimental tests of theory. Likewise, the integration of rapidly developing theory and experimental approaches from recent work on the invasion criterion, trophic dynamics and priority effects could help researchers face the challenge of disentangling the role of local species interactions and dispersal in shaping diversity patterns. These advances promise to provide new insights from empirical studies, inform the development of theory, and enhance our understanding of metacommunity dynamics.

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Supplementary material (available online as Appendix oik-03018 at <www.oikosjournal.org/appendix/oik-03018>). Appendix 1–2.