A process-based framework for metacommunity ecology

Patrick L. Thompson[1*]
Laura Melissa Guzman[1,2]
Luc De Meester[3]
Zsófia Horváth[3,4,5]
Robert Ptacnik[4]
Bram Vanschoenwinkel[6,7]
Duarte S. Viana[8,9]
Jonathan M. Chase[8,10]

*corresponding author - patrick.thompson@zoology.ubc.ca
[1]Department of Zoology & Biodiversity Research Centre, University of British Columbia, Canada
[2]Department of Biology, Simon Fraser University, Canada
[3]Laboratory of Aquatic Ecology, Evolution and Conservation, KU Leuven, Leuven, Belgium
[4]WasserCluster Lunz - Biologische Station, Lunz am See, Austria
[5]Balaton Limnological Institute, Centre for Ecological Research, Tihany, Hungary
[6]Department of Biology, Vrije Universiteit Brussel, Belgium
[7]Centre for Environmental Management, University of the Free State, South Africa
[8]German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig
[9]Leipzig University, Ritterstraße 26, 04109 Leipzig, Germany
[10]Department of Computer Sciences, Martin Luther University, Halle-Wittenberg

Keywords: dispersal, abiotic niche, competition, diversity, stability, regional, local, temporal, environmental change, coexistence

Statement of authorship: This project was conceived at the sTURN working group, of which all authors are members. PLT developed the framework and model with input from all authors. PLT wrote the model code. PLT and LMG performed the simulations. PLT produced the figures and wrote the first draft with input from LMG and JMC. All authors provided feedback and edits on several versions of the manuscript.

Data accessibility: All code for running the simulation model and producing the figures will be archived on Zenodo upon acceptance and the doi will be included at the end of the manuscript.

Abstract

The metacommunity concept has greatly advanced our understanding of how spatial dynamics shape ecological communities. To date, this framework has emphasized discrete differences between mechanisms structuring metacommunities (e.g. niche vs. neutral), despite the recognition that assembly processes are continuous. Here we present a fundamental reconception of the framework that explicitly links local coexistence theory to metacommunity theory and allows for a continuous range of competitive metacommunity dynamics. These dynamics emerge from the underlying processes that shape the dynamics of ecological communities: 1) density-independent responses to abiotic conditions, 2) density-dependent biotic interactions, and 3) dispersal. We also incorporate stochasticity in the demographic realization of each of these processes. The traditional metacommunity archetypes exist as discrete regions within this space, but our framework highlights a range of dynamics that are missed in classic metacommunity theory. We formalize this framework using a simulation model that explores the full range of competitive metacommunity dynamics by varying the strength of the underlying processes. We illustrate how the different processes interactively shape the diversity, functioning, and stability of metacommunities. This process-based framework extends the rich history of metacommunity ecology and can be used to generate testable hypotheses on the processes structuring metacommunities in nature.

Introduction

Recent decades have seen a shift from a primarily local perspective on species coexistence via interspecific interactions to include regional processes such as habitat heterogeneity, dispersal, and ecological drift within metacommunities (e.g. Levins & Culver 1971; Hubbell 2001; Mouquet & Loreau 2002; Amarasekare 2003)**.** These advances have allowed a deeper understanding of how species vary in their relative abundances and co-occurrence across spatial scales, as well as the influence of these on biodiversity patterns and ecosystem functioning (reviewed in Holyoak *et al.* 2005; Leibold & Chase 2018).

In building theory to understand how local and regional processes interact in metacommunities, a number of simplifying assumptions have been made. Hanski and Gyllenberg (1997) incorporated habitat heterogeneity and colonization/extinction dynamics, but ignored species interactions. Hubbell's (2001) neutral model incorporated dispersal and ecological drift, but ignored interspecific niche differences. And Tilman's (1982) resource-ratio model (see also Tilman & Pacala 1993) incorporates local species interactions and environmental variation, but largely ignored stochasticity and dispersal. Indeed, there are dozens of metacommunity models that incorporate fundamentally different assumptions about how species interact, trait differences among species, and aspects of dispersal and stochasticity (overviewed in Leibold & Chase 2018).

In an initial synthesis, Leibold et al. (2004) categorized the divergent theories into four archetypes based on their assumptions and outcomes: neutral, species sorting, patch dynamics, and mass effects. While this categorization was useful, it led to the perception that these are the key ways that metacommunities are structured. As empirical tests were developed to test them as alternative hypotheses (e.g. Cottenie 2005), studies focused largely on the matching of data to the predictions of the archetypes.

An alternative way to achieve synthesis in metacommunity theory is by emphasizing a series of core processes that each vary in strength among metacommunities. Loreau et al. (2003)

demonstrated how dispersal limitation, species sorting, and mass effects emerge from the same model by varying rates of dispersal. Likewise, Gravel et al. (2006) demonstrated how niche-like and neutral-like dynamics are opposite ends of a continuum defined by the degree to which species overlap in their abiotic niches. These findings reflect the increasing appreciation of a focus on the processes and their variation along continua (e.g. Vellend 2010; Logue *et al.* 2011; Vellend 2016; Leibold & Chase 2018).

A series of models have recently been developed that are capable of generating the metacommunity archetypes by altering key parameters (e.g. dispersal, niche breadth, species interactions, stochasticity), bringing us closer to the goal of redefining metacommunity theory based on processes (e.g. Shoemaker & Melbourne 2016; Fournier *et al.* 2017). These models each include elements that build towards a general process-based framework, but as of yet, none have fully reached this goal. That is, a model that 1) is based on continuous processes rather than discrete combinations of parameters that correspond to the different archetypes, 2) relaxes the simplifying assumption that all species compete equally for resources, 3) is spatially explicit and applicable to any landscape structure, and 4) is abundance-based, including dynamics at the local scale.

Here we develop a metacommunity framework that incorporates all of these elements. Our framework is based on three fundamental processes, as well as stochasticity in how they impact demography: 1) Density-independent responses to abiotic heterogeneity (i.e. the abiotic niche). This determines how local abiotic conditions affect each species' performance in the absence of competition. 2) Density-dependent biotic interactions, focusing on competition. Intraspecific and interspecific competition for resources limits population growth and affects local scale species coexistence. 3) Dispersal. Immigration and emigration alter local population sizes. We separate processes based on whether their effects on populations depend on density. This distinction is critical, because density-independent and dependent processes affect population dynamics and species coexistence in fundamentally different ways (Chase & Leibold 2003). While stochasticity is a critical feature of our framework, we do not consider it as a separate process, but instead include stochasticity in abiotic conditions, as well as in demography (which depends on the abiotic responses, biotic interactions, and dispersal). By distinguishing processes in this way, we can capture all metacommunity dynamics in a single mathematical framework and move between them by modifying the strength of these processes.

A general framework for competitive metacommunities

We formalize a metacommunity as a set of local communities where populations of multiple species potentially compete and can disperse among local communities that are distributed in space. Figure 1 depicts a schematic of such a metacommunity, visualizing a landscape in which local communities are separated via an uninhabitable matrix and connected via dispersal. Nevertheless, it is important to recognize that all communities exist within a metacommunity characterized by differences in scale (i.e. local and regional), heterogeneity, and dispersal, and so our framework applies much more broadly. We overview four basic propositions that form the foundation for a generalized metacommunity theory.

1) The density-independent growth rate of a population depends on the local abiotic conditions (Figure 1a). Density-independent growth in the absence of intra- or interspecific competition is determined by the dimensions of the abiotic environment (e.g. temperature, rainfall) that influence organism performance, but where the organisms do not impact that abiotic dimension (Tilman 1982; Chase & Leibold 2003). Thus, density-independent growth defines the range of conditions that allow for positive intrinsic growth (i.e. fundamental niche; Hutchinson 1957). In classic models (e.g. Lotka-Volterra), density-independent growth is expressed using a constant (e.g. r).

Abiotic conditions vary in space and time, resulting in differences in density-independent growth (r) depending on the shape of the species' abiotic niche. Abiotic niches are often thought to have a Gaussian shape, but they can take any form, including skewed (e.g. thermal performance curves) or positive (e.g. growth over increasing nutrient supply). When abiotic niche curves are narrow over the range of abiotic conditions, species will respond strongly to this variation (closer to the assumptions of classical 'niche-based' theory). In contrast, if abiotic niches are broad or flat over the range of abiotic conditions experienced, species will respond weakly or not at all (closer to the assumptions of neutral theory).

Density-independent responses to environmental conditions have been the focus of most niche-based metacommunity models (e.g. Loreau *et al.* 2003; Gravel *et al.* 2006; Shoemaker & Melbourne 2016; Fournier *et al.* 2017). However, density-independent responses to the environment are only one aspect of the realized niche, and this has led to confusion in how niche processes govern the dynamics of metacommunities. Coexistence within a habitat patch is more likely when species have similar density-independent growth rates, because it makes equal fitness (sensu Chesson 2000; Godoy & Levine 2014) more likely. But, local scale coexistence also requires stabilizing density-dependent biotic interactions or dispersal (Chesson 2000; Snyder & Chesson 2004).

2) *The realized growth rate of a population depends on the density-dependent intra- and interspecific interactions* (Figure 1b). Density-dependent competition limits species growth and, along with density independent abiotic responses, determines equilibrium abundances (i.e. carrying capacity Verhulst 1838; Lotka 1922; Volterra 1926). Most niche-based metacommunity theory assumes that species do not differ in their resource use (i.e. equal intra- and interspecific competition), but rather their competitive ability depends only on their density-independent match with the local environment (e.g. Loreau *et al.* 2003; Gravel *et al.* 2006; Shoemaker & Melbourne 2016; Fournier *et al.* 2017; Worm & Tittensor 2018; but see Liautaud *et al.* 2019). Yet, we know from local coexistence theory and empirical evidence that this is rarely the case (Chesson 2000; Adler *et al.* 2018). Density-dependent competition results because organisms impact resource availability (e.g. space, nutrients, water availability, prey). The density-dependent interaction strength of any species with its competitors for shared resources depends on the degree of overlap in resource use (sometimes termed 'niche differentiation'; Chesson 2000).

The biotic aspect of the niche has very different implications for community dynamics compared to the density-independent abiotic niche responses outlined above. In classic Lotka-Volterra models, density-dependent interactions are expressed using the $\alpha_{i,j}$, which is the per capita impact of species *j* on species *i*. $\alpha_{i,j}$ is a phenomenological parameter and is just one way that density-dependent biotic interactions can be expressed (Tilman 1982; Letten *et al.* 2017), but is useful to understand how biotic interactions can lead to a range of dynamics.

In a community of two species that have equal intraspecific competition (i.e. $\alpha_{i,i} = \alpha_{j,j}$), equal density-independent growth (i.e. $r_i = r_j$), and thus equal equilibrium abundance, four different outcomes are possible within a single habitat, depending on the balance of inter- (i.e. $\alpha_{i,j}$) to intraspecific (i.e. $\alpha_{i,i}$) competition (Dorschner *et al.* 1987):

a) stable coexistence - species compete more strongly with themselves than with each other (i.e. $\alpha_{j,i} < \alpha_{i,i}$ and $\alpha_{i,j} < \alpha_{jj}$),

b) competitive exclusion - competition is unbalanced (i.e. $\alpha_{j,i} > \alpha_{i,i}$ and $\alpha_{i,j} < \alpha_{j,j}$) so that the superior competitor *i* excludes the inferior species *j*, regardless of initial abundances,

c) multiple local equilibria - species compete with each other more strongly than with themselves (i.e. $\alpha_{j,i} > \alpha_{i,i}$ and $\alpha_{i,j} > \alpha_{j,j}$) so that the species with higher initial abundance excludes the other species,

d) equal competition - individuals of all species compete equally (i.e. $\alpha_{j,i} = \alpha_{i,i} = \alpha_{i,j} = \alpha_{j,j}$), so that coexistence is unstable, but exclusion is slow and determined by stochastic processes.

Of course, the outcome of competition becomes more complicated in more diverse communities (Barabás *et al.* 2016; Saavedra *et al.* 2017), when species have different strengths of intraspecific competition, and have different density-independent growth rates (Godoy & Levine 2014). Nevertheless, these four outcomes set the context for the dynamics of multispecies communities by determining whether local scale communities have single or multiple attractors.

Because density-dependent biotic interactions are strong determinants of local scale dynamics, they also influence how species respond to environmental change. This is because density-independent abiotic environmental factors can alter the abundance of interacting species, which effectively modifies density-dependent interactions (Ives & Cardinale 2004). These indirect effects of the environment are often strong in empirical communities (Davis *et al.* 1998; Alexander *et al.* 2015), but are absent from models assuming that species all interact equally. By including density-dependent biotic interactions, we can explore how the range of community dynamics that result from biotic interactions at local scales influence, and are influenced by, metacommunity processes.

3) *The size of a population depends on dispersal* (Figure 1c). Dispersal modifies the dynamics of local populations and communities both directly and indirectly. Emigration reduces population size, while immigration increases population size, and can bring in species that, through their density-dependent biotic interactions, strongly impact community structure. Furthermore, dispersal provides additional mechanisms that can allow species to coexist at local scales (Chesson 2000; Snyder & Chesson 2004).

Along a gradient from low to high dispersal, we expect to see the following processes (Mouquet & Loreau 2003):

a) low dispersal rates result in dispersal limitation, where spatial isolation prevents potential colonizers
b) intermediate dispersal allows species to colonize new habitats, allowing for environmental tracking, rescue effects, and recolonization
c) high dispersal rates facilitate source-sink dynamics where immigration lifts local population densities beyond the level that could be achieved based on local environmental conditions.

Multiple dispersal-mediated processes are likely to occur simultaneously within a metacommunity, especially when patches are not equally connected (Thompson *et al.* 2017).

Dispersal is a spatially explicit process that depends on the spatial connectivity of landscapes, the distance between habitats, species dispersal traits (e.g. dispersal rate and kernel), and population sizes. Metacommunity models have typically been spatially implicit for tractability, but explicit space can be an important determinant of dynamics (e.g. Fournier *et al.* 2017; Thompson *et al.* 2017).

Because dispersal alters population sizes, it also alters the realized strength of density-dependent processes and competition (Holt 1985). Likewise, population sizes alter the number of dispersing individuals, creating a feedback between dispersal and biotic interactions. This contrasts with the view that dispersal, the abiotic environment, and the biotic environment form a series of hierarchical filters to determine community assembly (e.g. Vellend 2016).

4) *Births, deaths, immigration, and emigration are stochastic processes that prevent metacommunity dynamics from being purely deterministic.* Stochasticity is inherent to any ecological system (McShea & Brandon 2010; Vellend 2016). Yet, rather than incorporating it as a separate process per se (e.g. Vellend 2016), we consider it to be an element of each of the three processes; this is because biological processes are probabilistic resulting in stochasticity in demography and dispersal (Shoemaker *et al.* 2019). This view of stochasticity aligns with the long history of models that have included it via probabilistic draws of the underlying biological processes (e.g. Levins & Culver 1971; Hubbell 2001; Matias *et al.* 2012; Shoemaker & Melbourne 2016; Fournier *et al.* 2017). Stochasticity in environmental conditions then alters metacommunity dynamics via the three processes (Shoemaker *et al.* 2019).

Delineating the range of possible competitive metacommunity dynamics

We illustrate this framework of a continuum of processes in three-dimensional space, with the axes referring to density-independent abiotic responses, density-dependent biotic interactions, and dispersal (Figure 2). While such an illustration is imperfect because these processes are not strictly one dimensional (e.g. dispersal depends on both rate and distance), it is a useful heuristic that allows us to compare and relate different metacommunity dynamics across this three-dimensional parameter space. The first axis is defined by the strength of density-independent abiotic responses. At one extreme, species have no response to abiotic heterogeneity (i.e. flat abiotic niches) and at the other extreme, heterogeneity results in large differences in density-independent growth (i.e. narrow abiotic niches). The second axis is defined by the degree to which competition for resources is stabilizing (i.e. $\alpha_{i,j} < \alpha_{i,i}$), equal (i.e. $\alpha_{i,j} = \alpha_{i,i}$), or destabilizing (i.e. $\alpha_{i,j} > \alpha_{i,i}$). The final axis is defined by the probability of dispersal, ranging from no dispersal to the limit where all individuals disperse in every time step. Within a given metacommunity, it is possible that species will differ in their positioning on these axes, for example if species have different dispersal rates, abiotic niche breadths, and competitive strengths.

The traditional organization of metacommunity theories into archetypes (Leibold *et al.* 2004) is consistent with this framework. In articulating them based on the three defining processes, we can see how they relate to one another (Figure 2). It also illustrates that these traditional archetypes encompass only a small subset of the possible parameter space of dynamics (Figure 2); other theories have explored some of the interactive space between the archetypes (e.g. Leibold & Chase 2018), but it is clear that there is much more conceptual space to explore. To place the archetypes within this space, we outline the assumptions (both explicit and implicit) that each makes about the three core processes emphasized here.

Neutral dynamics

The neutral archetype assumes that species have equal density-independent responses to abiotic heterogeneity, that density-dependent competition between species is equal, and that dispersal limitation is acting (i.e. dispersal is not high enough to homogenize the metacommunity) (Figure 2). Equal density-independent responses can be the result of indifference to environmental heterogeneity (i.e. flat abiotic niches) (e.g. Hubbell 2001) or of species having identical responses to abiotic heterogeneity (e.g. Gravel *et al.* 2006). Critically, this archetype implicitly assumes that competition between species is equal. Because of these particularly limiting assumptions, neutral dynamics occur only in a very confined region of our metacommunity parameter space.

Species sorting and mass effects

The species sorting archetype assumes that density-independent responses to abiotic heterogeneity are strong and that they differ amongst species (Figure 2). It makes no explicit assumptions about density-dependent biotic interactions, although many models assume equal inter and intraspecific competition (but see Chase & Leibold 2003; Thompson & Gonzalez 2017). Finally, the archetype implicitly assumes that dispersal is sufficient so that species can access favourable habitat patches, but that dispersal is not so high as to homogenize the metacommunity. The mass effects archetype makes these same assumptions, but in this case, dispersal rates are higher, allowing populations to persist in habitats that are otherwise unsuitable for growth (Figure 2).

Patch dynamics

The patch dynamics archetype has more complicated assumptions, including interspecific variation in competitive ability (e.g., stronger competitors exclude weaker competitors when they are both present in the same habitat patch). Classic models were agnostic to whether these competitive differences were due to density-dependent or density-independent processes (Levins & Culver 1971; Hastings 1980; but see Tilman 1994) . More recently, models have included the assumption of competitive differences in density-independent responses to the abiotic environment (i.e. competitively dominant species have higher density-independent growth), while assuming that density-dependent biotic interactions are equal (e.g. Shoemaker & Melbourne 2016; Fournier *et al.* 2017). Nevertheless, it is equally possible that such competitive exclusion can arise from unbalanced density-dependent competition (i.e. $\alpha_{i,j} > \alpha_{i,i}$ and $\alpha_{j,i} < \alpha_{j,j}$), with equal density-independent abiotic responses. This is how we have modelled the competition-colonization trade-off here (see Figure 2). For species to coexist in the patch dynamics archetype, we must also assume that there is a competition-colonization trade-off; species persist regionally because competitively weaker species have a higher probability of dispersing. Patch dynamics also implicitly assumes the occurrence of periodic disturbances, be they stochastic extinctions or environmental perturbations that cause local extirpations.

Beyond the archetypes

Our focus on model parameters highlights how the classical archetypes only encompass a small subset of this three-dimensional range of metacommunity dynamics (Figure 2). A number of dynamics that may occur in natural metacommunities do not fit neatly within the existing archetypes. Some of these dynamics have been modelled by combining aspects of the existing archetypes (reviewed in Leibold & Chase 2018)(e.g. patch dynamics with species sorting), or by including dispersal limitation, local resource partitioning, and priority effects (Fukami *et al.* 2016). Other combinations of parameters are likely but have not been modelled explicitly; our framework allows us to acknowledge and explore this undefined space.

Model description

The framework we discussed above is quite general and can accommodate a number of different formalizations. For our purposes here, we formalized these assumptions into a simulation model using Beverton-Holt discrete time logistic population growth with Lotka-Volterra competition and spatially explicit dispersal. The model simulates abundance-based population dynamics of *S* interacting species in *M* habitat patches, coupled by dispersal (Figure 1d, e). Thus, after accounting for density-independent responses to the abiotic environment, density-dependent competition (following Beverton & Holt 1957), and dispersal, $\hat{N}_{ix}(t+1)$ is the expected population size of species *i* in patch *x* at time $t+1$:

1) $$\hat{N}_{ix}(t+1) = N_{ix}(t)\frac{r_{ix}(t)}{1+\sum_{j=1}^{S}\alpha_{ij}N_{jx}(t)} - E_{ix}(t) + I_{ix}(t),$$

where $N_{ix}(t)$ is the population size at time *t*.

Proposition 1, *the density-independent growth rate of a population* $r_{ix}(t)$ *depends on the abiotic conditions at that location and time*. We have assumed that the abiotic environment is defined by a single variable that varies across space and time, and that $r_{ix}(t)$ is a Gaussian function of this environmental gradient such that

2) $$r_{ix}(t) = r_{max}e^{-\left(\frac{z_i - env_x(t)}{2\sigma_i}\right)^2},$$

where r_{max} is the maximum density independent growth rate, z_i is the environmental optimum of species *i*, $env_x(t)$ is the environmental conditions in patch *x* at time *t*, and σ_i is the abiotic niche breadth, which determines the rate at which growth is reduced by a mismatch between z_i and $env_x(t)$. We manipulate the strength of density-independent responses to abiotic heterogeneity through the parameter σ_i. When σ_i is small, the abiotic niche is narrow and so performance drops quickly when species are present in suboptimal environmental conditions. In contrast, when σ_i is large, the abiotic niche is broad. As σ_i becomes larger relative to the range of environmental conditions in the landscape, the abiotic niche effectively becomes flat, so that species growth is unaffected by environmental heterogeneity. This follows the common assumption of Gaussian abiotic niches, but other abiotic response shapes could be used (e.g. skewed unimodal curves, saturating, or monotonic). Furthermore, multiple response curves could be combined to incorporate multiple abiotic gradients.

Proposition 2, *the realized growth rate of a population depends on the density-dependent interactions between members of that population as well as with individuals of other species*. This is represented by the per capita interaction coefficient α_{ij}. When $j = i$ (i.e. α_{ii}), it represents the per capita rate of intraspecific competition for species *i*, and when $j \neq i$, it represents the per capita effect of interspecific competition of species *j* on species *i*. We generate different competitive scenarios by manipulating the relative strength of inter α_{ij} and intraspecific α_{ii} competition. We assume that these interaction coefficients are fixed across time and space—in effect assuming that resource supply is constant and equal across all patches (Tilman 1982). Relaxing this assumption would complicate the model and is beyond the scope of this paper but would explore how spatial variation in biotic interactions alters metacommunity dynamics.

Proposition 3, *the size of a population depends on dispersal*, which is incorporated via the emigration terms $E_{ix}(t)$ and immigration $I_{ix}(t)$ terms. $E_{ix}(t)$ is the number of individuals of species *i* dispersing from patch x at time *t*. This is determined by a random draw from a Poisson distribution with an expected value of $N_{ix}(t)a_i$, where a_i is the dispersal probability for individuals of species *i*. Here, we assume that a_i is equal across all species. Relaxing this assumption would be a worthwhile next step, but in general we expect that interspecific variation in dispersal should lead to fitness differences, which would erode the potential for coexistence unless additional trade-offs are assumed (e.g. competition-colonization trade-off). $I_{ix}(t)$ is the number of individuals of species *i* that arrive via immigration to patch x at time *t* from other patches. We assume that the probability of an individual arriving from another patch decreases exponentially with the geographic distance between patches:

3) $$\hat{I}_{ix}(t) = \sum_{y \neq x}^{M} E_{iy}(t)^{-L_i d_{xy}}$$,

where $\hat{I}_{ix}(t)$ is the expected value of $I_{ix}(t)$, d_{xy} is the geographic distance between patches x and y, and L_i is the strength of the exponential decrease in dispersal with distance. $I_{ix}(t)$ is determined by a random draw from a Poisson distribution with an expected value of $\hat{I}_{ix}(t)$.

Note that $\sum_{x=1}^{M} E_{ix}(t) = \sum_{x=1}^{M} \hat{I}_{ix}(t)$, so total expected immigration and realized emigration for each species are equal, and that realized immigration and realized emigration are equal on average.

Proposition 4, *births, deaths, immigration, and emigration are stochastic processes that prevent metacommunity dynamics from being purely deterministic*. Stochasticity is incorporated in two ways. First, through the stochastic component of immigration and emigration as noted above. Second, because we determine the realized population size in the next time step $N_{ix}(t+1)$ by drawing from a Poisson distribution with an expected value of $\hat{N}_{ix}(t+1)$ (following Shoemaker & Melbourne 2016). The Poisson draw also ensures that integer population sizes.

Simulation details

The results presented are based on model simulations of $M = 100$ patch metacommunities with a starting total species richness of $S = 50$ species and an r_{max} of 5 for all species .

Metacommunity spatial structure

We assume that habitat patches are distributed randomly in geographic space with their coordinates drawn from uniform distributions with the range [1, 100] (following Fournier *et al.* 2017; Thompson *et al.* 2017)(Figure S1). We convert these coordinates into a torus to avoid edge effects. Although we chose to restrict our simulations to this one metacommunity size and structure, the model can be run using any number of patches and any spatial structure. Our qualitative results appear robust to variation in species number and metacommunity size, based on initial sensitivity analyses (results not shown) and the fact that portions of our results are qualitatively consistent with other models (e.g. Hubbell 2001; Loreau *et al.* 2003; Mouquet & Loreau 2003; Gravel *et al.* 2006).

Environmental heterogeneity

We assume that the abiotic environment in a given patch varies continuously between 0 and 1 and is both spatially and temporally autocorrelated (Figure S1, S2). We generate this environmental heterogeneity with an exponential covariance model, using the *RMexp* function in the *RandomFields R* package (Schlather *et al.* 2015). We assume a mean environmental value across time and space of 0.5, an environmental variance of 0.5, and spatial and temporal scales of environmental autocorrelation of 50 and 500, respectively. The model can be easily modified to incorporate other patterns of changes of environmental conditions in time and space.

Initialization

We initialize the simulation by seeding each habitat patch with populations of each species drawn from a Poisson distribution where $\lambda = 0.5$. Thus, species start in a random subset of patches and at different abundances. We repeat this seeding procedure every 10-time steps over the first 100-time steps, giving each species the opportunity to establish if they can increase from low abundance. Their ability to do so will depend on whether they are suited to the local environmental conditions and their interactions with other species. By seeding the metacommunity randomly, we allow for the possibility of priority effects (but only if the structure of local competition allows for this, otherwise communities will converge in the same environmental conditions). To allow communities to reach equilibrium initially, we hold the environmental conditions in each patch constant for the first 200-time steps, while allowing for spatial variation in conditions.

Simulation runs

We ran each simulation for a total of 2200-time steps. This included the 200-time step initialization and an additional 500-time step burn in period. This duration contained sufficient temporal variation in environmental conditions and community composition to capture dynamics that were representative of particular parameters in the simulation. For each randomly generated landscape structure, we contrasted a range of dispersal rates a_i, crossed factorially with a range of abiotic niche breadths σ_i, crossed factorially with four different structures of competitive effects. To cover the full range from effectively disconnected to highly connected metacommunities, we varied 15 rates of dispersal, equally distributed in log space from 0.0001 to 0.464. We varied 13 values of niche breadth, equally distributed in log space from 0.001 to 10. These values were chosen to cover the range from so narrow as to preclude species persistence in variable environments to so broad that they are effectively neutral over the range of conditions experienced in the metacommunity. For simplicity, and to make fitness differences solely dependent on fundamental niche match, we assume that all species have the same strength of intraspecific competition $\alpha_{ii} = 1$. This is, however, not a necessary condition for generating the dynamics in our model, with the exception of the purely neutral case. The four different structures of competitive effects were:

1) equal competition; $\alpha_{ij} = \alpha_{ii}$,
2) local coexistence; $\alpha_{ij} < \alpha_{ii}$ and α_{ij} is drawn from a uniform distribution in the range [0, 0.5],
3) multiple local equilibria; values of α_{ij} are drawn from a uniform distribution in the range [0, 1.5]. This results in a combination of species pairs that can stably coexist, where one will exclude the other, or for which priority effects are possible.
4) competition-colonization trade-off; values of α_{ij} are drawn from a uniform distribution in the range [0, 1], except for 30% of species, which are considered dominant species. For the dominant species, $\alpha_{ij} > \alpha_{ii}$, and these values are drawn from a uniform distribution in the range [1, 1.5]. Thus, local coexistence is possible for subdominant species, but not between subdominant and dominant species. Coexistence between dominants and subdominants occurs at the regional scale, via the classic competition-colonization trade-off (Hastings 1980). For this, we assume that dispersal rates a_i are an order of magnitude lower for the competitive dominant species compared to the value used for all other species in the community. We also assume that each population has a probability of 0.002 of stochastic extirpation. In this way, this competitive scenario differs from the consistent and continuous assumptions from all other scenarios. Nevertheless, because the competition-colonization trade-off has an integral place in metacommunity theory, we include it here for two reasons. First, to demonstrate how such a trade-off can be incorporated in our framework and model (note that other implementations of such a tradeoff are also possible; e.g. Tilman 1994; Shoemaker & Melbourne 2016; Fournier *et al.* 2017). Second, to explore the dynamics that emerge from this trade-off across a range of assumptions about abiotic niche responses and dispersal rates.

For each of the 15 replicate landscapes, we ran all dispersal rates and abiotic niche breadth scenarios on the same four sets of randomly generated competitive competition coefficients.

Response variables

All response variables were based on the dynamics in the simulated metacommunities (e.g. Figure S3, S4) after excluding the first 700-time steps to avoid initial transient dynamics. Table 1 provides an overview of the metacommunity properties that we calculated in each simulation run, which include multiple richness and abundance metrics and their temporal stability. Simulations were performed in Julia (Bezanson *et al.* 2017) and figures were produced using *ggplot2* in *R* (R Development Core Team 2017). Example dynamics based under different combinations of parameters can be explored in this Shiny app - https://shiney.zoology.ubc.ca/pthompson/meta_com_shiny/

Results and Discussion

Our overarching message, both with the broader conceptual framework and more specific simulations, is that metacommunity dynamics exist along a continuum of processes rather than as discrete archetypes based on disparate assumptions. This continuum can be defined by three processes—1) density-independent responses to abiotic heterogeneity, 2) density-dependent competition, and 3) dispersal—as well as stochasticity in how they impact community dynamics. The framework generates the dynamics that define the four classic archetypes, but also a wide range of dynamics that do not fit within the archetypes, particularly when we relax the assumption of equal competition. We find that the structure of density-dependent competition has as large an effect on the dynamics of metacommunities as does dispersal and density independent responses to abiotic conditions, which have been the focus of most metacommunity theory to date. Fully exploring the wide range of dynamics in our model is beyond the scope of a single paper. Instead, we will structure our presentation by discussing the dynamics that result from the three processes, and the patterns of diversity, abundance, and stability that they produce. We also highlight key insights from previous metacommunity theory, illustrating how these results correspond to specific assumptions about the three processes of our framework.

The relationship between α, β, and γ-diversity

One classic result regarding how dispersal rates influence local (α-) and regional (γ-) diversity, as well as the turnover of species from site to site (β-diversity) comes from Mouquet and Loreau (2003) and Loreau et al. (2003). We can reproduce those predictions (Figure 3a), when we match their assumptions that species have differential and strong responses to abiotic conditions (i.e. narrow abiotic niches), but compete equally for a common resource (i.e. equal inter and intraspecific competition; e.g. σ_i = 0.5 and equal competition). With low dispersal, communities are effectively isolated and so different species establish in each patch (low α-, high spatial β-, high γ-diversity) and persist through time (low temporal β-diversity). Because competition is equal, local coexistence is not possible in the absence of dispersal. As dispersal increases, spatial β- and γ-diversity erode, communities have higher turnover through time (temporal β-diversity), and α-diversity increases. At higher dispersal rates, the metacommunity homogenizes due to mass effects, spatial and temporal β-diversity erodes, and further loss of γ-diversity results in losses in α-diversity. A key difference between our model and those of Mouquet and Loreau (2003) and Loreau et al. (2003) is that the spatially explicit nature of our model makes dispersal less effective at homogenizing the metacommunity and reducing γ-diversity because we assume that environmental conditions are spatially autocorrelated. Thus, mass effects tend to only allow individual species to dominate subregions of the metacommunity. Because real metacommunities are spatially explicit, we suggest that it is unlikely that dispersal can lead to full homogenization, except in metacommunities composed of a small number of very well-connected patches.

A broadly similar pattern emerges when species abiotic niches are so broad as to be effectively neutral (e.g. $\sigma_{i.}$ = 10; Figure 3b). Here, low dispersal rates again result in low α-diversity, but high spatial β- and γ-diversity, in this case, as a result of ecological drift rather than by the match with the abiotic conditions. Just as when abiotic responses are strong, increased dispersal erodes spatial β- and γ-diversity but increases α-diversity. Temporal β-diversity also increases as a result of stochastic colonization and extinction. Of course, just like in Hubbell's (2001) model, this diversity will very slowly decline without speciation or dispersal from outside of the metacommunity.

Relaxing the assumption of equal competition

Competition in real metacommunities is rarely, if ever, equal and this can result in a wide range of competitive outcomes (Dorschner *et al.* 1987; Ke & Letten 2018). If we assume that interspecific competition is weaker than intraspecific competition, we see that multiple species can coexist locally, even without dispersal (Figure 3c-d). This increased potential for coexistence means that higher rates of dispersal increase α-diversity, but do not erode γ-diversity as much as when competition is equal.

If we instead assume that interspecific competition can be either weaker or stronger than intraspecific competition, we also get species pairs that cannot coexist locally in the absence of mass effects (Ke & Letten 2018). In this competitive scenario, multiple different community compositions can be present in the same abiotic conditions, reflecting priority effects (Fukami *et al.* 2016). Priority effects are absent from the traditional archetypes but have been found to influence metacommunity structure (e.g. Shurin *et al.* 2004; Urban & De Meester 2009; Vass & Langenheder 2017; Toju *et al.* 2018). Notably, with this structure of competition, priority effects lead to spatial β-diversity, but these are eroded as dispersal homogenizes the metacommunity.

Finally, if we assume that there is a competition-colonization trade-off, subdominant species can only persist by colonizing newly disturbed patches before dominant species arrive. Because of the transient nature of these communities, all scales of diversity are lower and less predictable than in the other scenarios, but follow the same general pattern (Figure 3g,h). Here, we see dynamics that correspond to the classic patch dynamics archetype (Levins & Culver 1971) when we assume intermediate rates of dispersal and flat abiotic niche responses, which corresponds to the common assumption in patch dynamics models that the environment is homogeneous.

A more general α, β, and γ-diversity relationship

A more comprehensive view can be gained by viewing the relationship with abiotic niche breadth and dispersal at the same time (Figure 4). Here, we see that α-diversity is generally highest when dispersal rates are high, abiotic niches are wide, and interspecific competition is weaker than intraspecific competition. Spatial β-diversity is less sensitive to abiotic niche breadth but is greatest when dispersal is low and competition is strong (e.g. equal competition or multiple local equilibria). Temporal β-diversity is greatest when dispersal rates are intermediate, regardless of the structure of competition. But, the effect of abiotic niche breadth on these patterns does depend on the structure of competition. Finally, γ-diversity tends to peak under low dispersal rates, regardless of the abiotic niche breadth or the structure of competition, except for in the competition-colonization trade-off scenario.

The emergent properties of metacommunities as structured by the underlying processes

Contrasting all emergent metacommunity properties (e.g. diversity, abundance, and stability) listed in Table 1 together in multivariate space allows us to see how they are jointly structured by the three processes (Figure 5). The first three principal component axes together capture 89% of variation in the metacommunity properties. These axes broadly reflect variation in local scale community properties and stability (PC1 - 52%; linked to gradients in α-diversity, total community abundance, temporal-γ diversity, abundance invariability), spatial variation in community composition (PC2 - 23%; spatial β and γ-diversity), and temporal variation in community composition (PC3 - 14%; temporal β and γ-diversity).

The structure of competition is the principal driver of variation in simulated metacommunity dynamics captured by the three PCA axes, with each competition scenario falling out in a different region of multivariate space. The equal competition scenario is characterized by relatively low loadings and variation on the local properties axis (PC1; Figure 5a), but the highest variation and loadings on the spatial and temporal axes (PC2-3; Figure 5b). The local coexistence scenario is characterized by the largest variation and highest loading on the local properties axis (PC1), but relatively little variation and loading on the spatial and temporal axes (PC2-3). The multiple local equilibria scenario has moderate variation and loading on all axes. The competition-colonization trade-off scenario shows the lowest loading and variation on any of the axes, reflecting the low overall diversity that is maintained in these metacommunities. This sensitivity of metacommunity dynamics to the structure of local scale competition emphasizes the importance of this process in our metacommunity framework.

Whereas the structure of competition determines the general domain of metacommunity dynamics, dispersal and abiotic niche breadth can modify these dynamics. These modifications have, within the context of communities with equal competition, been the focus of most metacommunity theory to date. The principal effect of dispersal is to drive variation on the spatial and temporal axes (PC2-3; Figure 5b), although higher dispersal causes metacommunities to load slightly higher on the local properties axis (PC1; Figure 5a). Abiotic niche breadth has more moderate effects. Broader (more neutral) abiotic niches result in higher loadings on the local properties axis (PC1; Figure 5a) because they reduce fitness differences and so promote local coexistence. Abiotic niche breadth has no consistent impact on spatial β-diversity (PC2; Figure 5a,b), since high spatial β can be due to environmental heterogeneity (when abiotic niches are narrow) or stochasticity (when abiotic niches are broad). Broader abiotic niche breadth does seem to be linked to lower temporal β-diversity (PC3; Figure 5b). The exception is when competition is equal, in which case abiotic niche breadth has relatively little effect on temporal β-diversity. Together, this multivariate view illustrates how the three processes of our framework jointly generate a continuum of metacommunity dynamics.

Spatial insurance

The spatial insurance hypothesis predicts that intermediate rates of dispersal should reduce temporal variability in community abundance by allowing species to sort into their preferred habitats as the environment changes (Loreau *et al.* 2003). We find that this effect is strong under the assumptions of Loreau et al. (2003)(Figure 6; equal competition and relatively narrow niche breadth; e.g. σ_i = 0.5), but that it is eroded, lost, or even reversed with other combinations of abiotic niche breadths and biotic interactions. A more general result is that metacommunity abundance becomes more stable with increasing dispersal and with increasing niche breadth (Figure 6). A notable exception is that we see a U-shaped relationship between metacommunity stability and dispersal when multiple equilibria are possible and when abiotic niche breadths are nearly flat. This occurs because the strong interspecific interactions result in local compositional states that are relatively unstable and can change dramatically if dispersal introduces a new species that is incompatible with members of the local community.

The biodiversity-ecosystem functioning relationship

Understanding how dispersal influences the relationship between biodiversity and ecosystem functioning (BEF) is a key extension of metacommunity theory (Bond & Chase 2002; Loreau *et al.* 2003; Thompson & Gonzalez 2016; Leibold *et al.* 2017). A classic result is that α-diversity and community productivity are both maximized by intermediate rates of dispersal (Loreau:2003iz; see also Gonzalez *et al.* 2009; Shanafelt *et al.* 2015; Thompson & Gonzalez 2016). The same set of assumptions reproduce this result in our model when we use community abundance as a proxy for productivity (Figure 7; hump-shaped trajectory with equal competition and relatively narrow niche breadth; e.g. σ_i = 0.5). This result, however, depends on abiotic niche breadth and the structure of competition. The BEF relationship at local scales is relatively weak when competition is equal. This is because there is no complementarity in resource use, only complementarity in abiotic niche responses across time and space. Yet, when there is resource complementarity (Figure. 7; local coexistence), we see the positive and saturating BEF relationships that are common in empirical communities (Cardinale *et al.* 2011; Tilman *et al.* 2014). These BEF relationships remain present, but more variable when multiple equilibria are possible, and disappear entirely under a competition-colonization trade-off (Figure 7). Together, these findings provide a more comprehensive view of BEF relationships in metacommunities, showing that the strength of these effects can vary dramatically depending on the underlying mechanisms, and that they are particularly sensitive to how species compete for resources.

Caveats and future directions

Most metacommunity models and theory rely on the assumption that species are equivalent in all or most of their traits (Leibold & Chase 2018). This is most extreme in the neutral archetype (Hubbell 2001), but even niche-based models tend to assume that all species have the same dispersal rate, the same shape of the abiotic niche, and usually that competition is equal. Our model breaks one of these assumptions by exploring a range of competitive structures. However, with the exception of the competition-colonization trade-off scenario, we still assume equal dispersal rates and abiotic niche shape within an individual simulation. We did this to demonstrate how changes in dispersal and abiotic niche breadth alter metacommunity dynamics. In nature, however, there is high inter- and intraspecific trait variation, and this can greatly influence community dynamics (Bolnick *et al.* 2011; Violle *et al.* 2012; Roches *et al.* 2017). Exploring the outcome of this variation is an important next step that could easily be incorporated in our model and would allow for the identification of additional trade-offs that may be important for maintaining diversity when species differ in the way they respond to the environment, each other, and space. We did not allow for speciation in our model because it would not have greatly impacted dynamics over the timescales considered. However, it would be important over longer timescales, in particular in parameter combinations that would result in the gradual loss of regional diversity through ecological drift (e.g. Hubbell 2001).

While we have chosen to formalize our framework using Beverton-Holt dynamics with Lotka-Volterra competition, other modelling choices would be equally valid (e.g. Ricker model, resource competition model) provided they are consistent with the assumptions of our framework. In particular, our assumptions about the spatially explicit nature of dispersal could be modified to incorporate other dispersal patterns and processes, depending on the system of interest (Gibbs *et al.* 2010).

Our focus has been on the ecological dynamics of competitive metacommunities but extending this framework to include trophic dynamics would be a valuable next step. As outlined above, this could be done by including positive and negative per-capita interaction coefficients (Laska & Wootton 1998; Ives & Cardinale 2004) and different functional responses (Holling 1959). This extension will be critical to connect and synthesize trophic metacommunity ecology (e.g. Holt 2002; Gravel *et al.* 2011; Guzman *et al.* 2019) with the competitive theory that we have focused on here. In addition, a number of eco-evolutionary metacommunity models have been developed that have focused on the evolution of the density-independent responses of species to abiotic conditions (e.g. de Mazancourt *et al.* 2008; Loeuille & Leibold 2008; Vanoverbeke *et al.* 2015; Leibold *et al.* 2019; Thompson & Fronhofer 2019) or dispersal (e.g. Fronhofer *et al.* 2017). An important next step would be to examine how evolution of density-dependent biotic interactions affects the dynamics of metacommunities.

A critical measure of the value of our framework will be in its ability to provide insight into the dynamics of natural metacommunities. We see two ways how this can be achieved. First, our framework and model provide new hypotheses about how basic ecological processes influence metacommunity dynamics. These can be tested with observations and experiments to guide data analysis of empirical systems. Second, our model can be used to develop approaches that are informative for identifying the underlying structure of real metacommunities. For example, in a subsequent paper, we will use the model with a priori specified processes and then sample the resulting metacommunity time series as a ‘virtual ecologist’ to discern which analytical approaches and metrics are best for distinguishing the underlying processes in natural metacommunities.

Conclusions

Here, we have built on the rich history of the metacommunity concept for understanding patterns and processes of species co-occurrence, diversity, and a number of other responses. At the same time, our framework takes a fundamentally new perspective on the problem by focusing on the underlying processes, modelling the responses to three continuously varying processes—abiotic niche breadth, density-dependent biotic interactions, and dispersal—as well stochasticity in those processes. By defining our framework on processes, we not only can recreate results from each of the separate archetypes that have been central to metacommunity ecology, but can more transparently connect metacommunity theory with other dimensions of community ecology (e.g. coexistence theory, BEF research), and stimulate further advancement of our understanding of natural communities in a dynamic and changing world.

Acknowledgements

This paper resulted from the sTURN working group funded by sDiv, the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118). Additional funding came from Österreichische Forschungsgemeinschaft (ÖFG; International Communication, project 06/15539). We thank all members of the working group for discussions that inspired this manuscript and feedback in its development. PLT is supported by Killam and NSERC postdoctoral fellowships. LDM acknowledges KU Leuven Research Fund project C16/2017/002 and FWO project G0B9818. ZH acknowledges support by the Interreg V-A Austria-Hungary program of the European Regional Development Fund (project "Vogelwarte - Madárvárta 2") and GINOP 2.3.2.-15-2016-00057. LMG. is supported by NSERC CGS-D and UBC Four Year Fellowships. JMC was also supported by the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118). DSV was supported by the Alexander von Humboldt Foundation and sDiv, the Synthesis Centre of iDiv.

References

1.Adler, P.B., Smull, D., Beard, K.H., Choi, R.T., Furniss, T., Kulmatiski, A., *et al.* (2018). Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology Letters*, 85, 1265–11.

2.Alexander, J.M., Diez, J.M. & Levine, J.M. (2015). Novel competitors shape species' responses to climate change. *Nature*, 525, 515–518.

3.Amarasekare, P.B. (2003). Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters*, 6, 1109–1122.

4.Barabás, G., J Michalska-Smith, M. & Allesina, S. (2016). The Effect of Intra- and Interspecific Competition on Coexistence in Multispecies Communities. *Am Nat*, 188, E1–E12.

5.Beverton, R.J.H. & Holt, S.J. (1957). *On the Dynamics of Exploited Fish Populations*. Ministry of Agriculture, Fisheries and Food.

6.Bezanson, J., Edelman, A., Karpinski, S. & Shah, V.B. (2017). Julia: A Fresh Approach to Numerical Computing. *SIAM Rev.*, 59, 65–98.

7.Bolnick, D.I., Amarasekare, P.B., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., *et al.* (2011). Why intraspecific trait variation matters in community ecology. *Trends Ecol Evolut*, 26, 183–192.

8.Bond, E.M. & Chase, J.M. (2002). Biodiversity and ecosystem functioning at local and regional spatial scales. *Ecology Letters*, 5, 467–470.

9.Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., *et al.* (2011). The functional role of producer diversity in ecosystems. *Am J Bot*, 98, 572–592.

10.Chase, J.M. & Leibold, M.A. (2003). *Ecological Niches*. The University of Chicago Press, Chicago.

11.Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annu. Rev. Ecol. Evol. Syst.*, 31, 343–358.

12.Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters*, 8, 1175–1182.

13.Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature*, 391, 783–786.

14.de Mazancourt, C., Johnson, E. & Barrowman. (2008). Biodiversity inhibits species' evolutionary responses to changing environments. *Ecology Letters*, 11, 380–388.

15.Dorschner, K.W., Fox, S.F., Keener, M.S. & Eikenbary, R.D. (1987). Lotka-Volterra Competition Revisited - the Importance of Intrinsic Rates of Increase to the Unstable Equilibrium. *Oikos*, 48, 55–61.

16.Fournier, B., Mouquet, N., Leibold, M.A. & Gravel, D. (2017). An integrative framework of coexistence mechanisms in competitive metacommunities. *Ecography*, 40, 630–641.

17.Fronhofer, E.A., Nitsche, N. & Altermatt, F. (2017). Information use shapes the dynamics of range expansions into environmental gradients. *Global Ecol Biogeogr*, 26, 400–411.

18.Fukami, T., Mordecai, E.A. & Ostling, A. (2016). A framework for priority effects. *J Veg Sci*, 27, 655–657.

19.Gibbs, M., Saastamoinen, M., Coulon, A. & Stevens, V.M. (2010). Organisms on the move: ecology and evolution of dispersal. *Biology Letters*, 6, 146–148.

20.Godoy, O. & Levine, J.M. (2014). Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. *Ecology*, 95, 726–736.

21.Gonzalez, A., Mouquet, N. & Loreau, M. (2009). Biodiversity as spatial insurance: the effects of habitat fragmentation and dispersal on ecosystem functioning. In: *Biodiversity, Ecosystem Functioning and Ecosystem Services* (eds. Neem, S., Bunker, D., Hector, A., Loreau, M. & Perrings, C.). Oxford University Press, Oxford, pp. 134–146.

22.Gravel, D., Canham, C.D., Beaudet, M. & Messier, C. (2006). Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters*, 9, 399–409.

23.Gravel, D., Massol, F., Canard, E., Mouillot, D. & Mouquet, N. (2011). Trophic theory of island biogeography. *Ecology Letters*, 14, 1010–1016.

24.Guzman, L.M., Germain, R.M., Forbes, C., Straus, S., O'Connor, M.I., Gravel, D., *et al.* (2019). Towards a multi-trophic extension of metacommunity ecology. *Ecology Letters*, 22, 19–33.

25.Hanski, I. & Gyllenberg, M. (1997). Uniting two general patterns in the distribution of species. *Science*, 275, 397–400.

26.Hastings, A. (1980). Disturbance, coexistence, history, and competition for space. *Trends in Ecology and Evolution*, 18, 363–373.

27.Holling, C.S. (1959). The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly. *Can Entomol*, 5, 293–320.

28.Holt, R.D. (1985). Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology*, 28, 181–208.

29.Holt, R.D. (2002). Food webs in space: On the interplay of dynamic instability and spatial processes. *Ecological Research*, 17, 261–273.

30.Holyoak, M., Leibold, M.A. & Holt, R.D. (Eds.). (2005). *Metacommunities*. The University of Chicago Press, Chicago.

31.Hubbell, S.P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.

32.Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–422.

33.Ives, A.R. & Cardinale, B.J. (2004). Food-web interactions govern the resistance of communities after non-random extinctions. *Nature*, 429, 174–177.

34.Ke, P.-J. & Letten, A.D. (2018). Coexistence theory and the frequency- dependence of priority effects. *Nature Ecology and Evolution*, 1–7.

35.Laska, M.S. & Wootton, J.T. (1998). Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology*, 79, 461–476.

36.Leibold, M.A. & Chase, J.M. (2018). *Metacommunity Ecology*. Princeton University Press, Princeton, New Jersey.

37.Leibold, M.A., Chase, J.M. & Ernest, S.K.M. (2017). Community assembly and the functioning of ecosystems: how metacommunity processes alter ecosystems attributes. *Ecology*, 98, 909–919.

38.Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P.B., Chase, J.M., Hoopes, M.F., *et al.* (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7, 601–613.

39.Leibold, M.A., Urban, M.C., De Meester, L., Klausmeier, C.A. & Vanoverbeke, J. (2019). Regional neutrality evolves through local adaptive niche evolution. *P Natl Acad Sci USA*, 116, 2612–2617.

40.Letten, A.D., Ke, P.-J. & Fukami, T. (2017). Linking modern coexistence theory and contemporary niche theory. *Ecol Monogr*, 87, 161–177.

41.Levins, R. & Culver, D. (1971). Regional Coexistence of Species and Competition Between Rare Species (Mathematical Model/Habitable Patches). *P Natl Acad Sci USA*, 68, 1246–1248.

42.Liautaud, K., van Nes, E.H., Barbier, M., Scheffer, M. & Loreau, M. (2019). Superorganisms or loose collections of species? A unifying theory of community patterns along environmental gradients. *Ecology Letters*, 33, 1677–10.

43.Loeuille, N. & Leibold, M.A. (2008). Evolution in Metacommunities: On the Relative Importance of Species Sorting and Monopolization in Structuring Communities. *Am Nat*, 171, 788–799.

44.Logue, J.B., Mouquet, N., Peter, H. & Hillebrand, H. (2011). Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol Evolut*, 26, 482–491.

45.Loreau, M., Mouquet, N. & Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *P Natl Acad Sci USA*, 100, 12765–12770.

46.Lotka, A. (1922). Contribution to the energetics of evolution. *P Natl Acad Sci USA*, {8}, {147–151}.

47.Matias, M.G., Mouquet, N. & Chase, J.M. (2012). Dispersal stochasticity mediates species richness in source-sink metacommunities. *Oikos*, 122, 395–402.

48.McShea, D.W. & Brandon, R.N. (2010). *Biology's First Law: The Tendency for Diversity and Complexity to Increase in Evolutionary Systems*. The University of Chicago Press, Chicago.

49.Mouquet, N. & Loreau, M. (2002). Coexistence in metacommunities: The regional similarity hypothesis. *Am Nat*, 159, 420–426.

50.Mouquet, N. & Loreau, M. (2003). Community Patterns in Source-Sink Metacommunities. *Am Nat*, 162, 544–557.

51.R Development Core Team. (2017). R: A language and environment for statistical computing.

52.Roches, Des, S., Post, D.M., Turley, N.E., Bailey, J.K., Hendry, A.P., Kinnison, M.T., *et al.* (2017). The ecological importance of intraspecific variation. *Nature Ecology and Evolution*, 1–11.

53.Saavedra, S., Rohr, R.P., Bascompte, J., Godoy, O., Kraft, N.J.B. & Levine, J.M. (2017). A structural approach for understanding multispecies coexistence. *Ecol Monogr*, 87, 470–486.

54.Schlather, M., Malinowski, A., Menck, P.J., Oesting, M. & Strokorb, K. (2015). Analysis, Simulation and Prediction of Multivariate Random Fields with Package Random Fields. *J Stat Softw*, 63, 1–25.

55.Shanafelt, D.W., Dieckmann, U., Jonas, M., Franklin, O., Loreau, M. & Perrings, C. (2015). Biodiversity, productivity, and the spatial insurance hypothesis revisited. *J Theor Biol*, 380, 426–435.

56.Shoemaker, L.G. & Melbourne, B.A. (2016). Linking metacommunity paradigms to spatial coexistence mechanisms. *Ecology*, 97, 2436–2446.

57.Shoemaker, L.G., Sullivan, L.L., Donohue, I., Cabral, J.S., Williams, R.J., Mayfield, M.M., *et al.* (2019). Integrating the underlying structure of stochasticity into community ecology. *Ecology*, ecy.2922–44.

58.Shurin, J.B., Amarasekare, P.B., Chase, J.M., Holt, R.D., Hoopes, M.F. & Leibold, M.A. (2004). Alternative stable states and regional community structure. *J Theor Biol*, 227, 359–368.

59.Snyder, R.E. & Chesson, P. (2004). How the Spatial Scales of Dispersal, Competition, and Environmental Heterogeneity Interact to Affect Coexistence. *Am Nat*, 164, 633–650.

60.Thompson, P.L. & Fronhofer, E.A. (2019). The conflict between adaptation and dispersal for maintaining biodiversity in changing environments. *P Natl Acad Sci USA*, 116, 21061–21067.

61.Thompson, P.L. & Gonzalez, A. (2016). Ecosystem multifunctionality in metacommunities. *Ecology*, 97, 2867–2879.

62.Thompson, P.L. & Gonzalez, A. (2017). Dispersal governs the reorganization of ecological networks under environmental change. *Nature Ecology and Evolution*, 1, 0162.

63.Thompson, P.L., Rayfield, B. & Gonzalez, A. (2017). Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography*, 40, 98–108.

64.Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.

65.Tilman, D. (1994). Competition and Biodiversity in Spatially Structured Habitats. *Ecology*, 75, 2–16.

66.Tilman, D. & Pacala, S.W. (1993). The maintenance of species richness in plant communities. In: *Species Diversity in Ecological Communities* (eds. Ricklefs, R. & Schluter, D.). Chicago, pp. 13–25.

67.Tilman, D., Isbell, F. & Cowles, J.M. (2014). Biodiversity and Ecosystem Functioning. *Annu. Rev. Ecol. Evol. Syst.*, 45, 471–493.

68.Toju, H., Vannette, R.L., Gauthier, M.-P.L., Dhami, M.K. & Fukami, T. (2018). Priority effects can persist across floral generations in nectar microbial metacommunities. *Oikos*, 127, 345–352.

69.Urban, M.C. & De Meester, L. (2009). Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. *Proc. Biol. Sci.*, 276, 4129–4138.

70.Vanoverbeke, J., Urban, M.C. & De Meester, L. (2015). Community assembly is a race between immigration and adaptation: eco-evolutionary interactions across spatial scales. *Ecography*, 39, 858–870.

71.Vass, M. & Langenheder, S. (2017). The legacy of the past: effects of historical processes on microbial metacommunities. *Aquat. Microb. Ecol.*, 79, 13–19.

72.Vellend, M. (2010). Conceptual Synthesis in Community Ecology. *The Quarterly Review of Biology*, 85, 183–206.

73.Vellend, M. (2016). *The Theory of Ecological Communities*. Princeton University Press, Princeton, NJ.

74.Verhulst, P.-F. (1838). Notice sur la loi que la population poursuit dans son accroissement. *Correspondance Mathématique et Physique*, 113–121.

75.Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., *et al.* (2012). The return of the variance: intraspecific variability in community ecology. *Trends Ecol Evolut*, 27, 245–253.

76.Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically. *Nature*, 118, 558–560.

77.Worm, B. & Tittensor, D.P. (2018). *A Theory of Global Biodiversity*. Princeton University Press, Princeton, NJ.

Table 1. Metacommunity properties calculated from simulated dynamics. *S*, *M,* and *T* are the number of species, patches, and time points in the simulations, respectively. $S_x(t)$ is the number of species present in patch *x* at time *t*. $S(t)$ is the number of species present across all patches at time *t*. S_x is the total number of species present in patch *x* across all time points.

Property	Symbol	Equation	Description
α-richness	α	$\frac{\sum_{t=1}^{T}\frac{\sum_{x=1}^{M} S_x(t)}{M}}{T}$	Number of species in each patch at a given time
γ-richness	γ	$\frac{\sum_{t=1}^{T} S(t)}{T}$	Total number of species in the metacommunity at a given time
temporal-γ richness	γ-time	$\frac{\sum_{x=1}^{M} S_x}{M}$	Total number of species present locally across all time points
spatial β-richness	β-space	$\gamma - \alpha$	Spatial variation in community composition
temporal β-richness	β-time	$\gamma_{time} - \alpha$	Temporal variation in community composition
total community abundance	N	$\frac{\sum_{t=1}^{T}\frac{\sum_{x=1}^{M}\sum_{i=1}^{S} N_{ix}(t)}{M}}{T}$	Average number of individuals in a community at a given time. Note, metacommunity community abundance is *N*M* and so only differs in magnitude.
temporal α-abundance invariability	α-invar.	$\frac{\sum_{x}^{M}\frac{N_x}{\sigma_{Nx}}}{M}$	Temporal stability of community abundance
temporal γ-abundance invariability	γ-invar.	$\frac{N}{\sigma_N}$	Temporal stability of metacommunity abundance

Figures

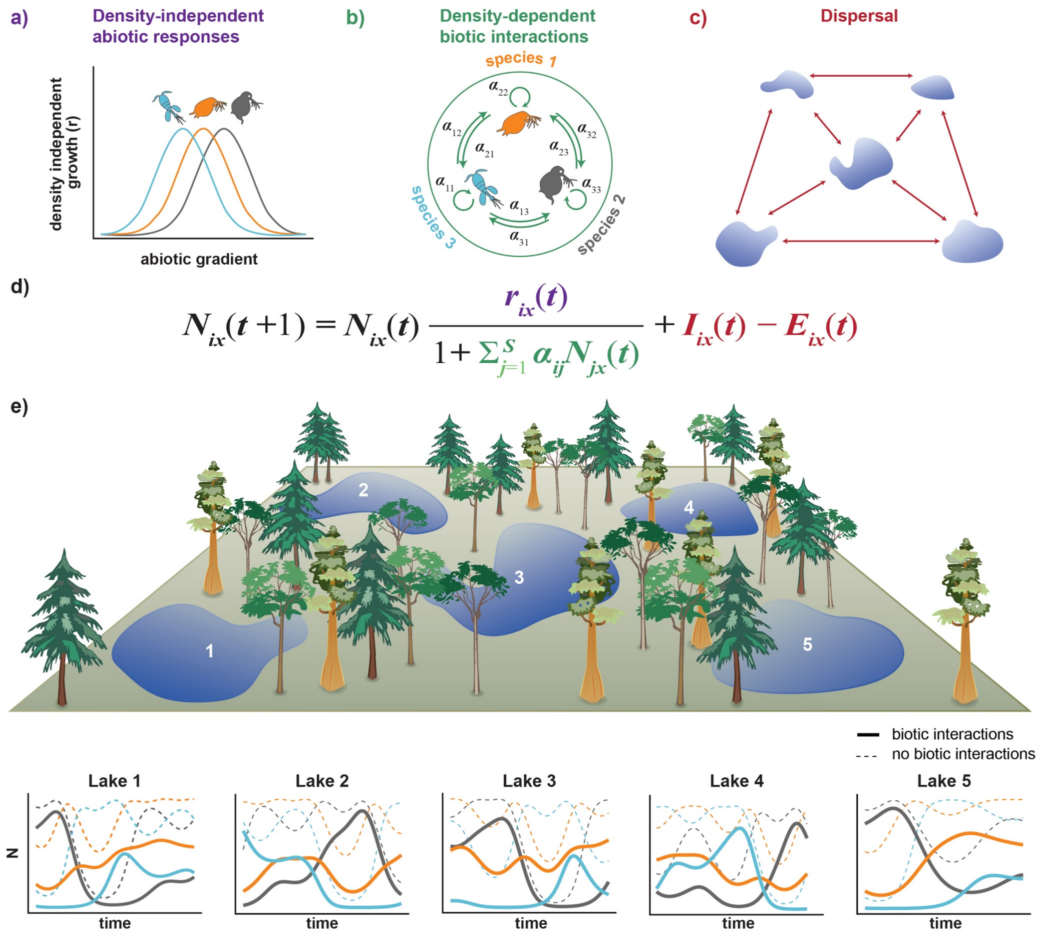

Figure 1. A schematic representation of our metacommunity framework and how we formalize each aspect of it in our mathematical model. a) Density-independent abiotic niches of three zooplankton species are represented graphically, where r_i follows a Gaussian response curve over the gradient of abiotic environmental conditions in the metacommunity, but each species *i* has a different environmental optimum. b) Dynamics also depend on interactions within and among species. This is included as per capita intraspecific α_{ii} interspecific α_{ij} interaction coefficients, and their realized impact on population dynamics increases with population size $N_{ix}(t)$. c) Dispersal alters population sizes via immigration and emigration and depends on the physical arrangement of habitat patches in the landscape. d) Each of these processes is expressed as separate expressions in our mathematical model. In this model, $N_{ix}(t)$ is the abundance of species *i* in patch *x* at time *t*, $r_{ix}(t)$ is its density-independent growth rate, α_{ij} is the per capita effect of species *j* on species *i*, $I_{ix}(t)$ is the number of individuals that arrive from elsewhere in the metacommunity via immigration, and $E_{ix}(t)$ is the number of individuals that leave via emigration. e) Simulated dynamics of a three zooplankton species, five lake metacommunity. The abiotic conditions vary across time and space and species respond to this heterogeneity via the Gaussian response curves in panel a. The species also compete so that the realized dynamics differ from those that would occur in the absence of interspecific

competition (thick solid vs. thin dashed lines). Dispersal connects populations via immigration and emigration, with more individuals being exchanged between lakes that are in close proximity. Although stochasticity in population growth and dispersal is integral to our framework and is included in all other simulations presented in this paper, we have omitted stochasticity from these dynamics to increase clarity. Figure design by Sylvia Heredia.

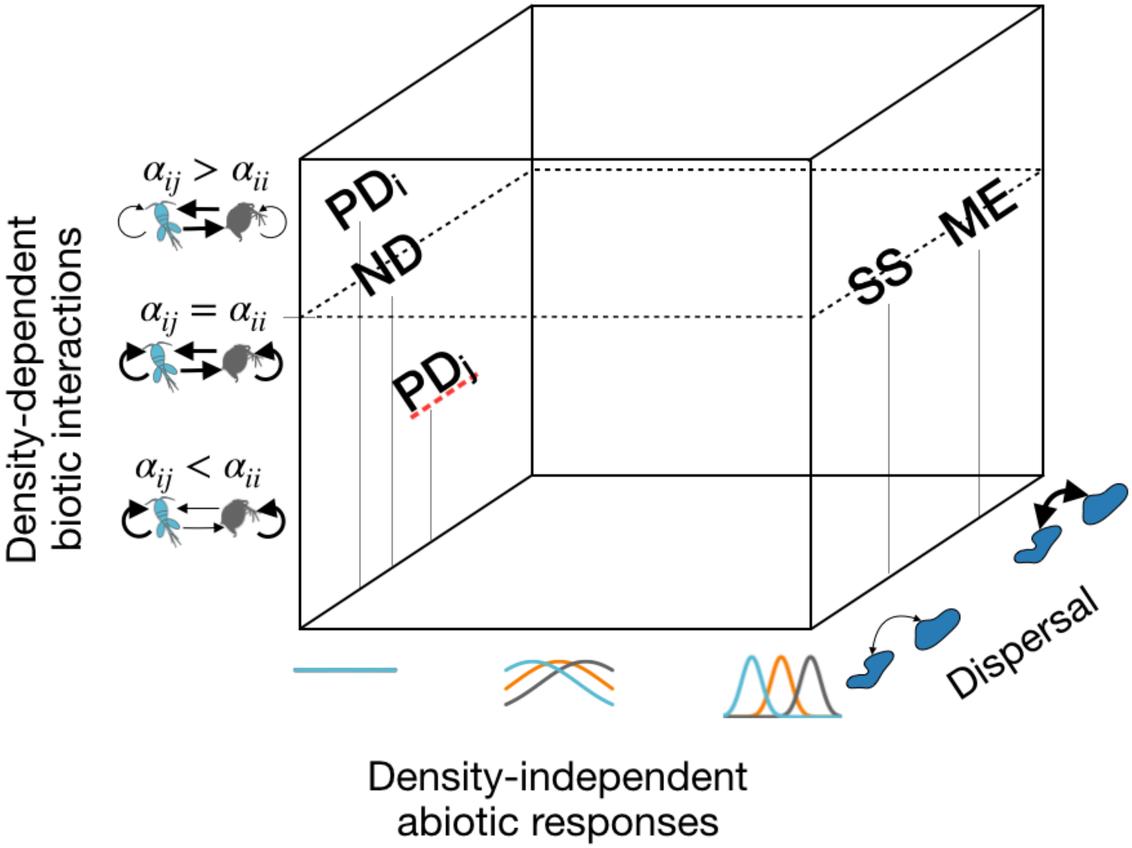

Figure 2. Illustration of the three dimensions of possible metacommunity dynamics. Three key dimensions of our framework define this space: 1) density-independent abiotic responses that range from a flat abiotic niche to narrow abiotic niches with interspecific variation in optima, 2) density-dependent biotic interactions that range depending on the relative strength of interspecific and intraspecific interactions, and 3) dispersal that ranges from very low dispersal rates to very high dispersal rates. The approximate location of each of the four original metacommunity archetypes: ND - neutral dynamics, PD - patch dynamics, SS - species sorting, and ME - mass effects, is indicated to illustrate how our framework links to previous theory. The lines below each label indicate their position in x,z space. PD$_i$ indicates the position for competitively dominant species with lower dispersal, PD$_j$ indicates the position for competitively weaker species with higher dispersal. Importantly, much of this space is undefined by the four archetypes but represents potential dynamics that can emerge from different combinations of the three processes of our framework.

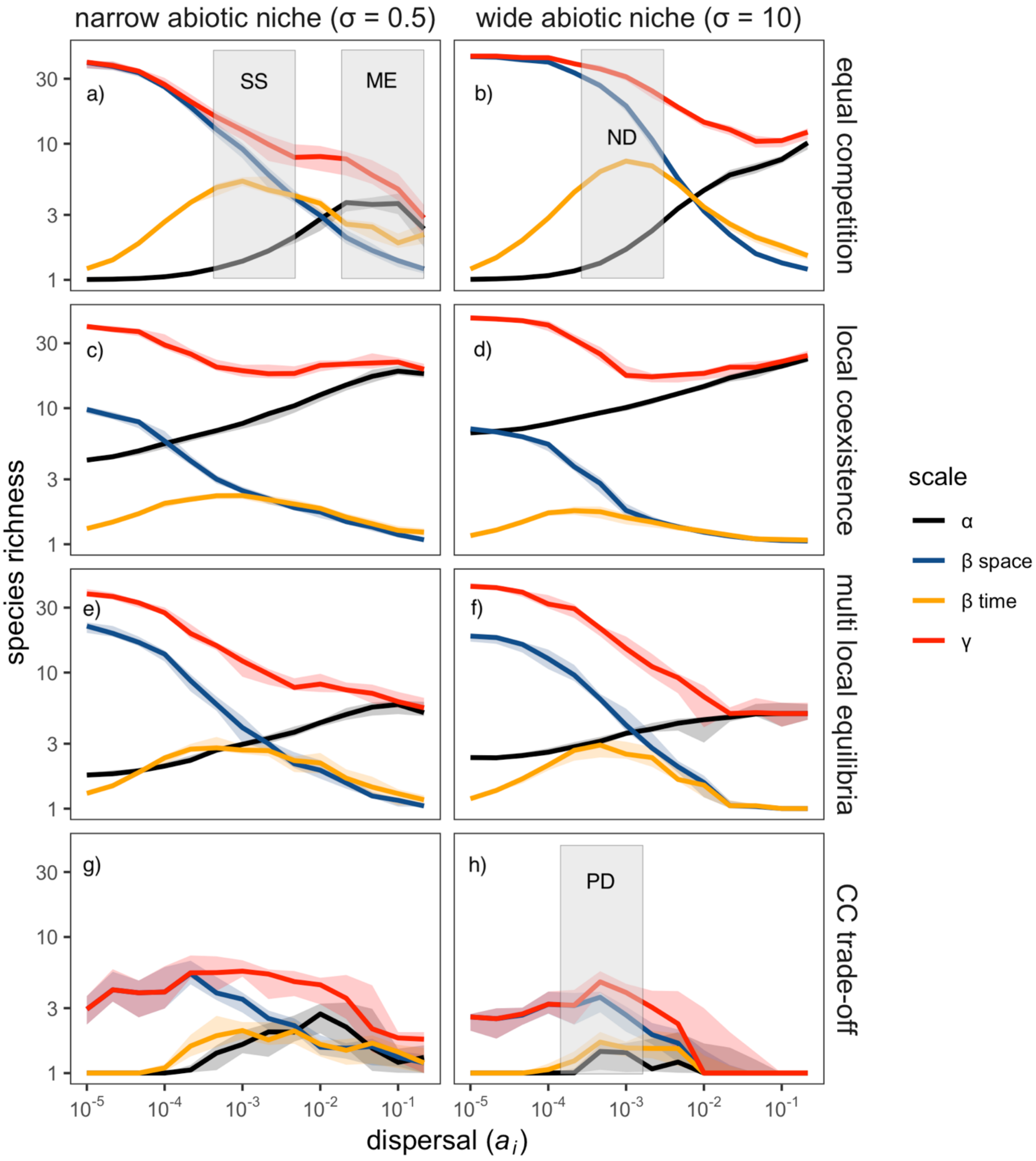

Figure 3. The relationship between dispersal a_i and α, β (spatial and temporal) and γ richness under narrow (column - σ_i = 0.5) and flat (column - σ_i = 10) abiotic niches across the four competitive scenarios (rows). The corresponding parameter space for each of the original metacommunity archetypes: ND - neutral dynamics, PD - patch dynamics, SS - species sorting, and ME - mass effects, is indicated with the shaded boxes. The interquartile range (bands) and median (solid lines) from 15 replicate simulations are shown.

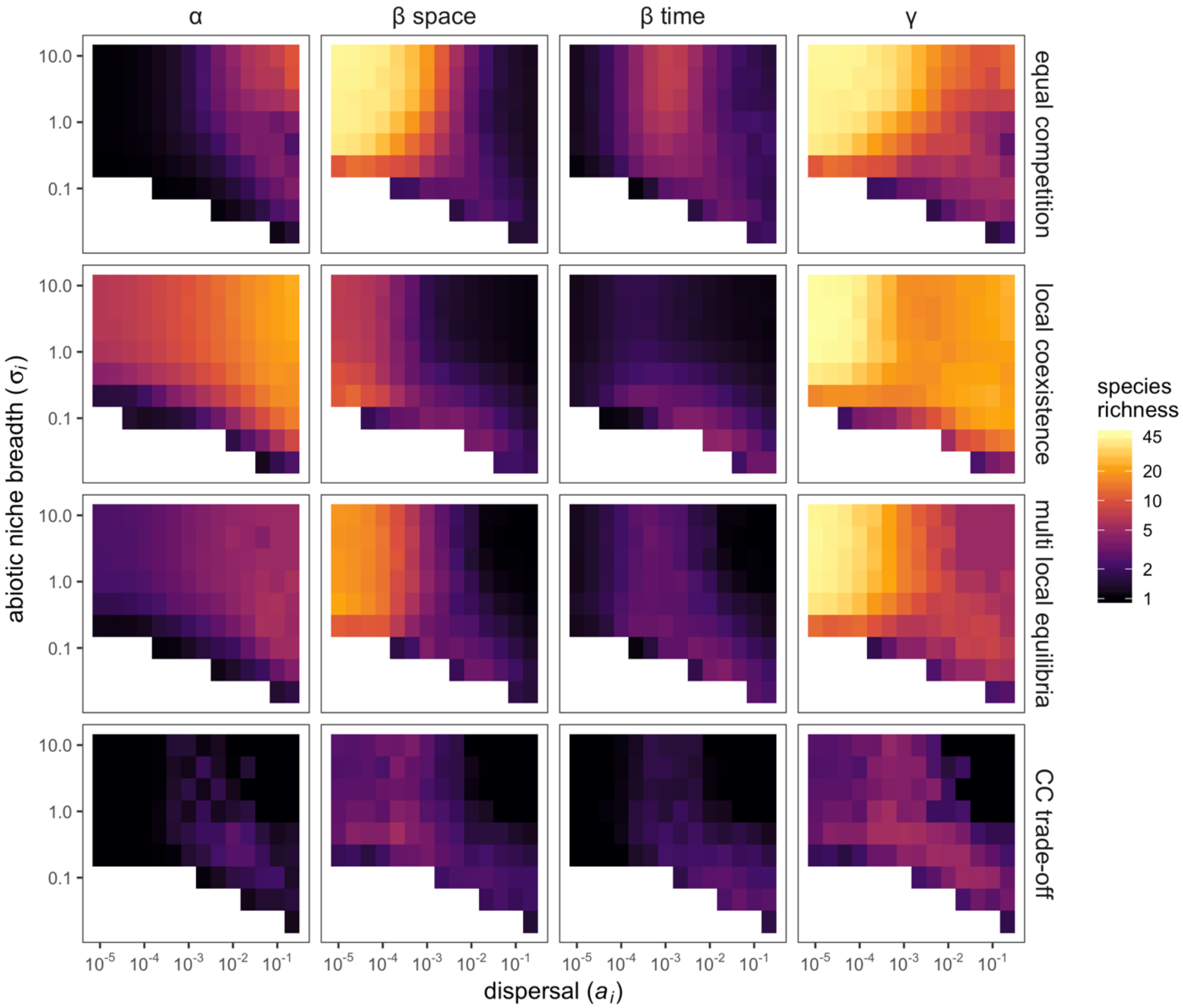

Figure 4. α, β (spatial and temporal), and γ richness (columns) across the full range of dispersal rates a_i (x-axis), abiotic niche breadth σ_i (y-axis), and competitive scenarios (rows). Each pixel represents the median value across 15 replicate simulation runs. Colours hues are spaced on a $\log_{10}$ scale (see legend). White space represents combinations of parameters where no species were able to persist. To see the dynamics that produce these patterns check out our interactive shiny app - https://shiney.zoology.ubc.ca/pthompson/meta_com_shiny/.

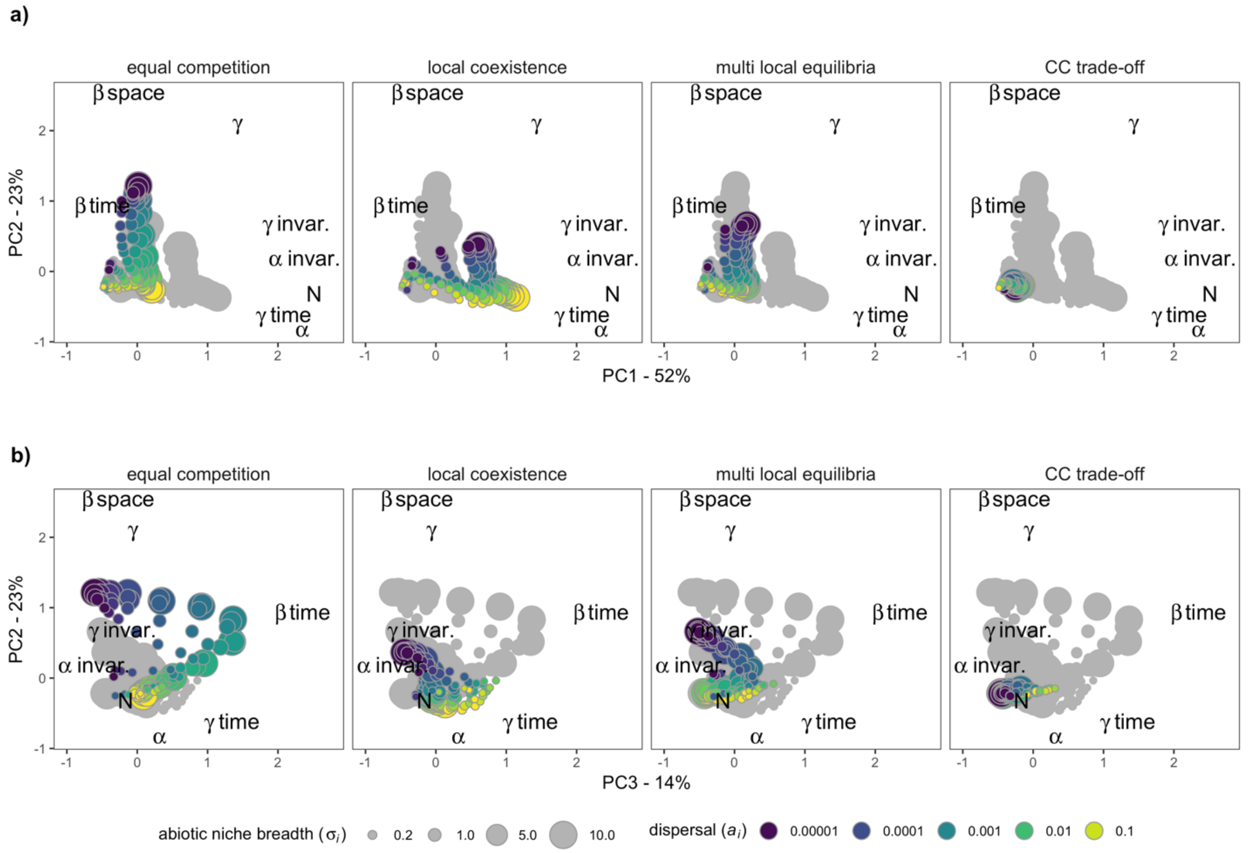

Figure 5. PCA (a; axes 1 and 2, b; axes 2 and 3) of metacommunity response variables, illustrating how dispersal a_i (colour of circles), the abiotic niche breadth σ_i (size of circles), and the structure of competition (the four panels) jointly result in variation in metacommunity properties. Each circle shows the median value across 5 replicate simulations of the response variables from a different set of parameters. The grey shading shows the full range of multivariate space occupied across all parameter combinations.

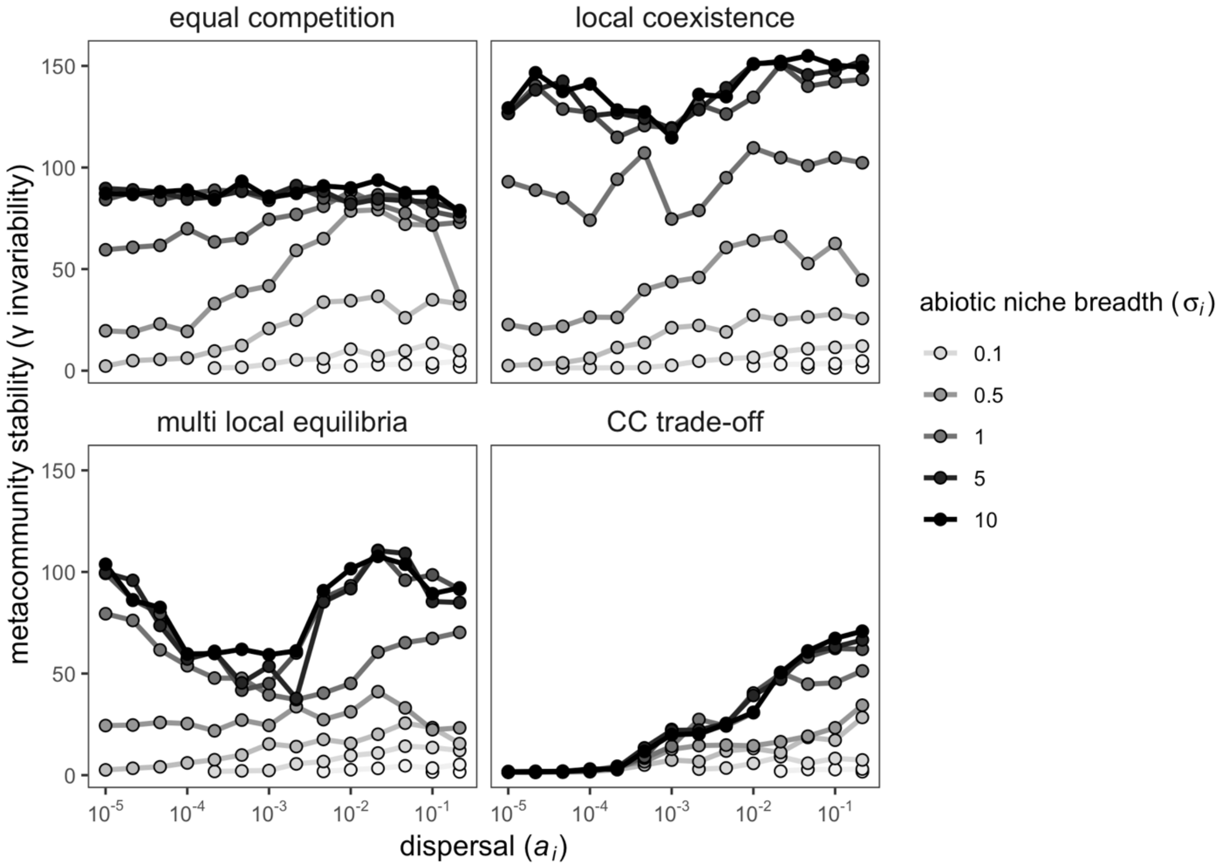

Figure 6. The spatial insurance relationship between dispersal and metacommunity scale stability in total biomass (invariability). Lines connect different dispersal rates a_i with the same abiotic niche breadth σ_i (color of lines and points). Values are medians from 15 replicate simulations. Legend shows the grey scale using a subset of σ_i values.

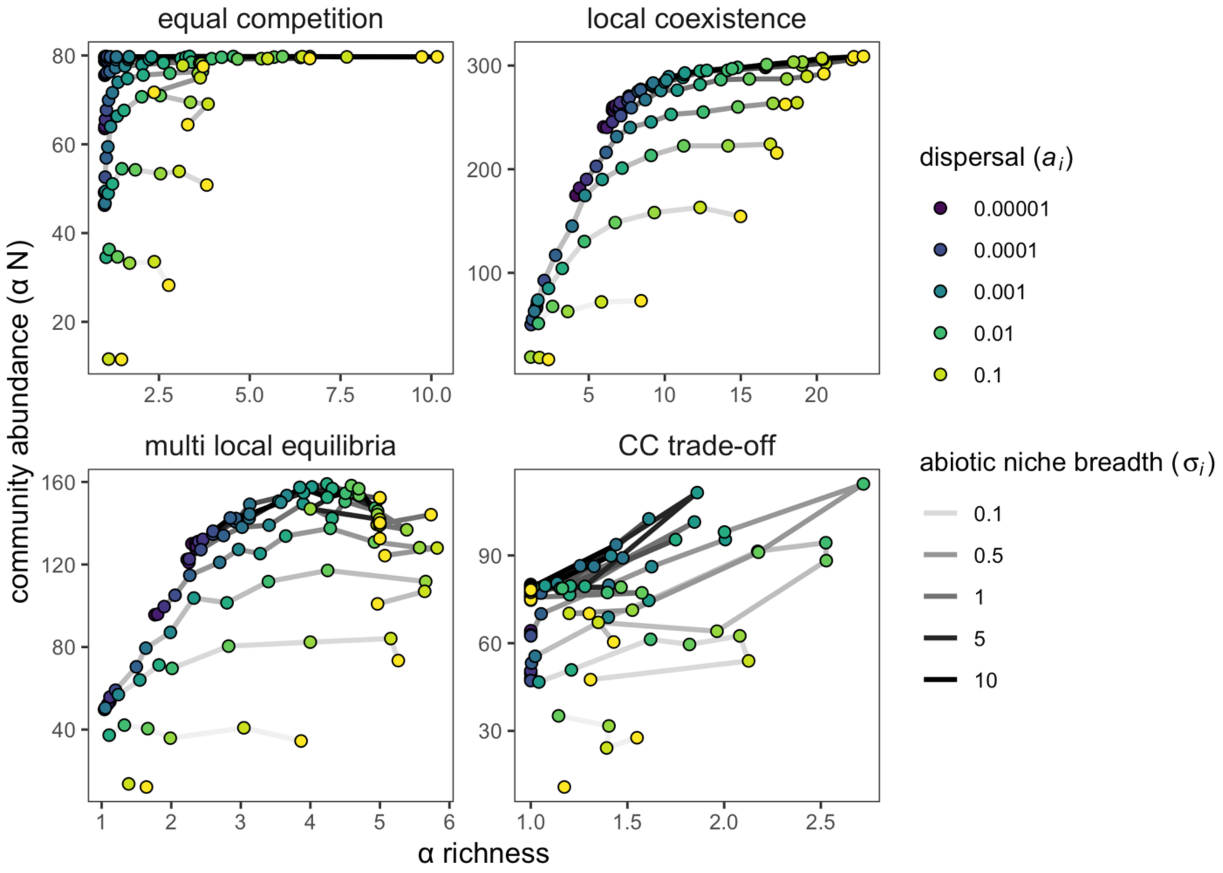

Figure 7. The biodiversity functioning relationship between α-diversity and community abundance *N*. Lines connect different dispersal rates a_i (color of point) with the same abiotic niche breadth σ_i (shade of line). Values are medians from 15 replicate simulations. Legend shows the grey scale using a subset of σ_i values and the colour scale using a subset of a_i values.