

# The multifactorial effects of dispersal on biodiversity in environmentally forced metacommunities

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**Abstract.** Disentangling the effects of dispersal and environmental heterogeneity on biodiversity is a central goal in ecology. Although metacommunity structure can be partitioned into spatial and environmental fractions, it remains unclear whether these statistical results can be used to infer the relative importance of dispersal limitation (spatial fraction) and environmental forcing (environmental fraction). Using an environmentally forced, spatially explicit metacommunity model, we show that the distinct effects of the mean (advection) and the standard deviation (diffusion) of the dispersal kernel on biodiversity are not easily detectable via variation partitioning alone. Although increasing dispersal ultimately leads to a decrease in the spatial fraction due to reduced dispersal limitation and greater species sorting, the magnitude of the spatial fraction depends on the complex interplay between the nature of dispersal and the type of boundary conditions in the metacommunity. Indeed, metacommunities characterized by either high or low dispersal can exhibit a small spatial fraction. A case study of a marine metacommunity experiencing strong alongshore transport is consistent with these findings, as the size of the spatial fraction is not associated with dispersal. Overall, our results suggest that accounting for the nature of environmental forcing as well as the multifactorial effects of dispersal is critical for understanding how ecological and environmental processes give rise to biodiversity across spatial scales.

**Key words:** dispersal; environmental gradients; metacommunity; rocky intertidal; source-sink dynamics; species sorting.

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## INTRODUCTION

Species abundance distributions are driven by a combination of abiotic and biotic processes operating at multiple spatial and temporal scales (Leibold et al. 2004, Holyoak et al. 2005). Although uncontroversial today, this synthetic perspective evolved from ardent and recurring debates about the relative influence of biotic (Elton 1927, Nicholson 1933) and abiotic (Grinnell 1917, Davidson and Andrewartha 1948, Andrewartha and Birch 1954) processes on patterns of species diversity and population dynamics (reviewed by Coulson et al. 2004). For

instance, pioneering work by Grinnell (1917) showed that species often track the geographical distribution of environmental conditions that characterize their habitat. In doing so, the Grinnellian niche perspective emphasized the importance of environmental heterogeneity as a driver of species abundance. This purely abiotic definition of the niche, which suggested a unidirectional effect of the environment on species, was later extended by Charles Elton, who highlighted the importance of biotic processes and the reciprocal feedbacks between species and their environment in dictating community structure (Elton 1927). A similar but more acrimonious argument

emerged about the drivers of population dynamics, with Andrewartha and Birch (1954) championing the role of density-independent abiotic factors such as temperature and Nicholson (1933) arguing for the dominance of density-dependent biotic interactions such as competition.

Although these debates initially focused on the relative importance of biotic and abiotic processes at local scales, the role of regional factors such as dispersal began to garner greater attention following the development of island biogeography (MacArthur and Wilson 1967). By modeling how species diversity on islands could depend on the balance between regional immigration from the mainland and local extinction rates, MacArthur and Wilson laid the foundation for metacommunity theory (Levins and Culver 1971, Hastings 1980, Tilman 1994), a framework which depicts ecological systems as sets of discrete communities of interacting species linked by dispersal (Leibold et al. 2004, Holyoak et al. 2005). Metacommunities are thus ideal for understanding how biotic and abiotic processes operating at multiple scales interact to give rise to patterns of biodiversity.

Modern theory has identified four main metacommunity perspectives based on the relative influence of local vs. regional (a)biotic factors on the distribution of species (Leibold et al. 2004, Holyoak et al. 2005). The patch dynamic perspective stresses the importance of tradeoffs between local and regional biotic processes as the drivers of community structure (Levins and Culver 1971, Tilman 1994). For instance, an interspecific competition–colonization tradeoff can allow an arbitrary number of species to persist on a single resource in a spatially structured but environmentally homogeneous habitat (Tilman 1994). On the other hand, the species sorting perspective focuses on the effect of spatial environmental heterogeneity in dictating the distribution of species. Specifically, by assuming that dispersal allows species to reach patches characterized by their preferred environmental conditions, this perspective emphasizes niche separation due to local competitive exclusion over spatial rescue effects (Leibold et al. 2004, Holyoak et al. 2005). The mass effects approach also considers patches to be environmentally heterogeneous but assumes that dispersal is sufficiently high to generate spatial dynamics that override local

competitive exclusion (Leibold et al. 2004, Holyoak et al. 2005). Indeed, when dispersal is high, the movement of individuals from source patches characterized by good environmental conditions can allow species to persist in sink patches characterized by poor environmental conditions (Pulliam 1988, Amarasekare and Nisbet 2001, Holyoak et al. 2005). Such source–sink dynamics can alter patterns of biodiversity in metacommunities (Mouquet and Loreau 2003) and erode the relationship between spatial environmental heterogeneity and the distribution of species. Finally, the neutral perspective, which often serves as a null model, assumes that all individuals are demographically equivalent and that community composition is driven by the combination of limited dispersal and ecological drift (Hubbell 2001).

The metacommunity perspectives outlined above have provided the foundation for recent theoretical developments identifying multiple dispersal-based coexistence mechanisms. These coexistence mechanisms all rely on distinct connectivity patterns arising from interspecific differences in spawning time, dispersal ability, or dispersal direction. For instance, interspecific differences in dispersal ability (Bode et al. 2011) or asymmetrical connectivity patterns (Salomon et al. 2010) can promote coexistence between competing species when environmental conditions are spatially homogeneous. Interspecific differences in temporal variability have also been identified as a coexistence mechanism in spatially homogeneous environments (Berkley et al. 2010). Here, differences in spawning time coupled with temporal variability in dispersal can promote coexistence by creating ephemeral spatiotemporal niches that promote the long-term coexistence of competing species (Berkley et al. 2010). Finally, Aiken and Navarrete (2014) extended the results of Berkley et al. (2010) and Salomon et al. (2010) by showing that differences in the dispersal properties of subordinate and dominant species could promote coexistence in competitive metacommunities.

Although metacommunity theory has defined different perspectives based on the relative importance of dispersal and environmental heterogeneity as drivers of biodiversity, testing this theory will require identification of statistical signatures of these underlying mechanisms in

observational data. However, given the necessary scope and scale, it is logistically impractical to conduct manipulative experiments in order to identify the drivers of metacommunity structure in the real world. One promising solution to this vexing problem is variation partitioning, a statistical technique commonly used to decompose community variation into spatial and environmental fractions (Borcard et al. 1992, 2004, Peres-Neto et al. 2006). Within this framework, the environmental fraction essentially measures the degree of correlation between local species abundances and abiotic factors such as temperature or rainfall. The spatial fraction largely represents the residual spatial variation in community structure not explained by the abiotic factors. The size of the spatial fraction is most commonly interpreted as the effect of dispersal, or more specifically, the degree of dispersal limitation, where low dispersal rates or geographical barriers can prevent species from reaching patches characterized by their optimal environmental conditions (Cottenie 2005, Flinn et al. 2010, Tuomisto et al. 2012). Although this statistical framework is powerful, there is still considerable debate about how to interpret the spatial and environment fractions in an ecologically meaningful way (Cottenie 2005, Gilbert and Bennett 2010, Tuomisto et al. 2012, Legendre and Gauthier 2014). For instance, in analyses of empirical and simulated datasets, dispersal limitation can lead to both large and small spatial fractions (i.e., high and low residual spatial variation in community structure respectively) (Cottenie 2005, Gilbert and Bennett 2010). Hence, bridging the gap between metacommunity theory and variation partitioning by identifying statistical signatures of biological and environmental factors will promote our ability to predict and manage the dynamics of complex and interconnected ecosystems.

Here, we use spatially explicit models to explore the ability of variation partitioning to detect a dispersal signal in environmentally forced metacommunities. Specifically, we found that although increasing advection (i.e., the mean of the dispersal kernel) or diffusion (i.e., the standard deviation of the dispersal kernel) ultimately leads to a decrease in the spatial fraction, the magnitude of the spatial fraction does not map

to the dispersal rate directly. Indeed, large spatial fractions can be associated with both high and low dispersal rates and the strength of the environmental gradient amplifies this inconsistency. These results hold in the presence of environmental noise as well as across a range of environmental gradients and are consistent with observational data from an intertidal metacommunity along the West Coast of the United States. Overall, our findings suggest that the interpretation of the spatial fraction does not map onto a particular process, but rather depends on the complex interaction between dispersal, boundary conditions, and strength of environmental forcing.

## MATERIALS AND METHODS

### *The model*

To determine how environmental heterogeneity and different aspects of dispersal affect patterns of species diversity and abundance, we developed a spatially explicit metacommunity model with lottery competition by extending Levins' classical spatially implicit framework (see Appendix S1: Fig. S1; Levins 1969, Levins and Culver 1971). This type of model is well suited for describing competition between sessile species with mobile dispersal stages in both terrestrial (e.g., plants; Tilman 1994, Mouquet and Loreau 2003) and aquatic ecosystems (e.g., invertebrates; Gouhier et al. 2010b, 2011). Each metacommunity consists of  $L$  distinct sites linked by propagule dispersal, a process that determines each of the  $S$  species' potential recruitment according to a Gaussian kernel whose advection and diffusion rates can be specified (Appendix S1: Fig. S1c, d). Although all species share the same dispersal kernel, their realized recruitment patterns depend on the match between a site's environment and each species' physiological requirements, depicted by a Gaussian distribution around an optimal environmental value (Appendix S1: Fig. S1b). Environmental heterogeneity was implemented as a simple linear gradient (Appendix S1: Fig. S1a). These processes were modeled using the following set of coupled ordinary differential equations, which track the abundance  $N_i$  of each species  $i$  at site  $x$  along a one-dimensional array of size  $L$ :

$$\frac{dN_i(x)}{dt} = r_i(x)F(e(x), o_i) \left( 1 - \sum_{j=1}^S N_j(x) \right) - m_i N_i(x) \quad (1)$$

Here, the first term on the right-hand side represents the realized recruitment rate of species  $i$  at site  $x$ , the second term in parentheses represents lottery competition for space, and the third term represents species-specific background mortality. The realized recruitment rate is the product of each species' potential recruitment rate  $r_i(x)$  and survivorship  $F$  in that environment  $e(x)$ . The potential recruitment rate  $r_i(x)$  is the convolution of the product of propagule production  $p_i(y)$  and density  $N_i(y)$  at each source site  $y$  with the dispersal kernel  $k$  at destination site  $x$ :

$$r_i(x) = \int_{-L/2}^{L/2} p_i(y) N_i(y) k(x-y) dy \quad (2)$$

Thus, the term  $r_i(x)$  denotes the total number of recruits arriving at each destination site  $x$  from all other source sites  $y$  via dispersal. The dispersal kernel itself is a normalized Gaussian distribution (i.e., sums to 1) with mean  $\mu$  and standard deviation  $\sigma$  (Siegel et al. 2003):

$$k(x) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(x-\mu)^2}{2\sigma^2}} \quad (3)$$

where  $\mu$  represents alongshore advection and  $\sigma$  represents diffusion. We manipulated both  $\mu$  and  $\sigma$  independently for each simulation, allowing us to control the extent (advection) and scale (diffusion) of dispersal. Each species' propagule survivorship is represented by a Gaussian curve centered around a species-specific environmental optimum  $o_i$  (Appendix S1: Fig. S1b) such that survivorship  $F$  of species  $i$  at site  $x$  is:

$$F(e(x), o_i) = e^{-\frac{(e(x) - o_i)^2}{2}} \quad (4)$$

Hence, the smaller the difference between a species optimum and the environment, the greater its propagule survivorship and realized recruitment rate.

Spatial environmental variation was modeled using a simple linear gradient:

$$e(x) = \begin{cases} ux & \text{if } x \leq L/2 \\ -ux & \text{if } x > L/2 \end{cases} \quad (5)$$

Here,  $u$  represents the slope of the linear environmental gradient. We simulated 10 different levels of  $u$  ranging from 0.02 to 0.16 in order to determine the robustness of our results to the strength of the environmental gradient. We also ran additional simulations that included random noise affecting local environmental conditions  $e(x)$  within each site  $x$  using a white noise (spatially uncorrelated) process to determine the robustness of our results to different levels of environmental stochasticity (Appendix S2):

$$e(x) = ux + v(x) \quad (6)$$

Here,  $v(x)$  represents environmental stochasticity via a random deviate drawn from a normal distribution with a mean of zero and a standard deviation ranging from 0 (no noise) to 1 (high noise). Running simulations for 10 uniformly spaced standard deviations between 0 and 1 allowed us to determine the robustness of our model results to variation in the linearity and stochasticity of the environmental gradient (Appendix S2).

### Model simulations

The model equations were solved numerically using an explicit Runge–Kutta (4, 5) formula in MATLAB (function `ode45`) for 2000 time steps. The metacommunity consisted of  $S = 20$  species competing across  $L = 140$  sites (absorbing boundary conditions) or  $L = 100$  sites (periodic boundary conditions). We varied the dispersal advection and diffusion rates independently to simulate the dynamics of species ranging from direct developers, whose propagules remain in their natal site (i.e., zero advection and diffusion), to long-distance dispersers (i.e., high advection or diffusion). For simulations manipulating the advection rate  $\mu$ , the diffusion rate was fixed at  $\sigma = \sqrt{10}$ . For simulations manipulating the diffusion rate  $\sigma$ , the advection rate was fixed at  $\mu = 0$ . We followed existing approaches (Mouquet and Loreau 2003) and used our model to simulate the simplest and most generic metacommunity scenarios. Specifically, initial abundances for all species were random across all sites, the same dispersal kernel was used for each species, and the propagule production rates  $p_i$  were randomly selected from a



uniform distribution with a minimum value of 5 and a maximum value of 10. The mortality rates  $m_i$  were selected so that each species had the same production-to-mortality ratio  $p_i/m_i$  in order to ensure coexistence in the absence of environmental heterogeneity and dispersal. Additionally, each species' environmental optimum  $o_i$  was selected randomly from a uniformly spaced vector of 20 values ranging from the minimum to the maximum environmental condition  $e(x)$ . Overall, adopting this approach allowed us to generate baseline and system-agnostic results. Simulations were run under one of two scenarios to explore the effects of boundary conditions. First, we used absorbing boundary conditions to simulate a finite-size linear environment where propagules are able to leave the system. Second, we used periodic boundary conditions to simulate an infinite-size environment without edge effects (Gouhier et al. 2010a, b, 2013). Here, the linear environmental gradient was thus altered in order to avoid sudden spatial discontinuities at the ends of the spatial domain. Specifically, the environmental gradient in our simulations increases linearly with slope  $u$  from the beginning of the spatial domain (i.e., site 1) to the middle (i.e., site 50) and then decreases linearly from the middle to the opposing end of the spatial domain (i.e., site 100) with slope  $-u$ . This ensures the two ends of the spatial domain (sites 1 and 100), which are in fact nearest neighbors under periodic boundary conditions, experience similar environmental conditions. To test the robustness of the model results to covariation in advection and diffusion, we also ran additional simulations where both aspects of dispersal (advection, diffusion) covaried as predicted under climate change (e.g., Gerber et al. 2014; see Appendix S3). All analyses were performed on final species abundances. Species whose final local abundances were lower than  $10^{-8}$  were considered to have gone extinct.

### Model analysis

The model results were analyzed using two complementary approaches. First, we used species' presence/absence information to partition biodiversity into local ( $\alpha$ ), between-community ( $\beta$ ), and regional ( $\gamma$ ) diversity using standard methods (Whittaker 1972, Mouquet and Loreau 2003). Here, regional diversity  $\gamma$  was measured as the total species richness across the entire

metacommunity, local diversity  $\alpha$  was measured as the average species richness within each site, and between-community diversity  $\beta$  was measured as the difference between regional and local diversity. Second, we used partial redundancy analysis (RDA) to partition species abundances across the metacommunity into their spatial ( $S|E$ ), environmental ( $E|S$ ), and shared ( $ENS$ ) fractions (Borcard et al. 1992, 2004, Peres-Neto et al. 2006). This was achieved by relating the matrix of species abundances  $Y$  to (1) the environmental matrix  $X_1$ , which consisted of the variables that characterized the environmental gradient, and (2) the spatial matrix  $X_2$ , which was created via a spectral decomposition of the spatial structure of the metacommunity using the principle coordinates of neighboring matrices (PCNM) method (Borcard et al. 2004). The environmental fraction  $E|S$  thus represents the spatial variation in community structure that is strictly due to the environment, whereas the spatial fraction  $S|E$  represents the "residual" spatial variation in community structure that cannot be explained by the environment. This method is particularly powerful because it can partition the spatial and environmental fractions of metacommunity structure even when the shared fraction  $ENS$  is large because the environment is spatially structured (Borcard et al. 1992, 2004, Peres-Neto et al. 2006). This is important given that the environment is strongly spatially structured in both our simulations and our test system, the intertidal metacommunity along the West Coast of the United States (Gouhier et al. 2010b).

### Empirical case study

We used community data from the rocky intertidal along the West Coast of the United States (Russell et al. 2006, Schoch et al. 2006, Gouhier et al. 2010b) to determine the empirical relationship between the spatial fraction and dispersal. This is an ideal test system because it is characterized by (1) strong latitudinal environmental gradients in sea surface temperature, primary production, and upwelling (Menge et al. 2004, Gouhier et al. 2010b, Menge and Menge 2013), and (2) the relatively rapid southward advective California Current (Hickey 1979, Huyer 1983, Largier et al. 1993). Data were collected annually from 2000 to 2003 at 48 sites ranging from southern California to northern Washington (32.7–48.4°N).

Community structure was determined by averaging the abundance of each species across 10 randomly placed 0.25-m<sup>2</sup> quadrats along 3–4 random transects at each site for the low, mid, and high zone (see details in Gouhier et al. 2010b). Environmental variables included chlorophyll-*a* concentration (chl-*a*, in mg/m<sup>3</sup>), upwelling index (m<sup>3</sup>/s/100 m of coastline), and mean annual sea surface temperature (SST, in °C). Data were obtained from the sea-viewing wide field of view sensor (SeaWiFS; NASA), from sea level pressure maps (Pacific Fisheries Environmental Laboratory), and from a high-resolution radiometer (NOAA), respectively (Gouhier et al. 2010b). Pelagic larval duration (PLD) is commonly used as a proxy for dispersal ability for sessile marine organisms, as directly assessing larval movement remains a challenge (Shanks et al. 2003, Siegel et al. 2003, Shanks 2009, Selkoe and Toonen 2011). For our empirical test, we used this approach to split the species found in our surveys into four distinct groups based on their dispersal potential: direct developers (0 d), low PLD (~8 d), intermediate PLD (~21 d), and high PLD (~70 d). We conducted variation partitioning for each group of species across all zones in this empirical dataset to determine the size of the spatial and environmental fractions. The approach we used was identical to the one used for the model simulations, where species abundances across the metacommunity were partitioned into their spatial ( $S|E$ ), environmental ( $E|S$ ), and shared ( $E \cap S$ ) fractions (Borcard et al. 1992, 2004, Peres-Neto et al. 2006).

## RESULTS

### *Patterns of biodiversity*

We begin by analyzing the closed version of the metacommunity model (i.e., self-recruitment only). Under this scenario, the following relationship between all pairs of species  $\{i, j\}$  must hold for coexistence to occur at equilibrium:

$$\frac{m_i(x)}{p_i(x)F(e(x), o_i)} = \frac{m_j(x)}{p_j(x)F(e(x), o_j)} \quad (7)$$

The ratio of mortality to realized recruitment must thus be identical across all species in order for coexistence to occur within each site  $x$ . Hence, in the absence of dispersal, an arbitrary number of species can coexist via a fitness equalizing

tradeoff between mortality and realized recruitment (sensu Chesson 2000). Because any species with a higher ratio is expected to competitively exclude all other species locally, environmental heterogeneity promotes species sorting by generating low within-site diversity  $\alpha$ , high between-site diversity  $\beta$ , and maximizing regional diversity  $\gamma$  (Fig. 1a, b; dispersal advection and diffusion rates = 0). This is because each species essentially monopolizes the site whose environmental conditions are closest to its optimum.

In general, the introduction of dispersal between sites generates the species diversity patterns commonly described in the literature (Mouquet and Loreau 2002, 2003, Shanafelt et al. 2015, Thompson and Gonzalez 2016). Here, the type of dispersal (advection vs. diffusion) and the nature of the boundary conditions (absorbing simulating a finite-size linear environment vs. periodic simulating an infinite-size environment) determine the structure of biodiversity in the metacommunity. As species are subject to the same linear gradient under each scenario (absorbing or periodic), differences only occur at high dispersal rates, which lead to lower recruitment rates (due to greater propagule loss) with absorbing boundary conditions and higher recruitment rates with periodic conditions, as species are able to reach parts of the spatial domain that are similar to their optimal environmental condition. Overall, the shapes of the species diversity curves are largely driven by the nature of dispersal whereas the heights of the curves are mediated by the boundary conditions (Fig. 1). In the absence of dispersal, our simulations confirm our analytical results: Self-recruitment generates a strong positive local feedback between adult abundance and propagule production that promotes species abundance in sites characterized by their optimal environmental conditions (Fig. 1). This promotes competitive exclusion and species sorting, which lead to low local diversity ( $\alpha$ ), high between-community diversity ( $\beta$ ), and high regional diversity ( $\gamma$ ). Increasing dispersal ( $0 < \mu < 3$ ,  $0 < \sigma < 5$ ) reduces the degree of self-recruitment and species sorting by generating a positive regional feedback between sites via spatial rescue effects (Brown and Kodric-Brown 1977). This leads to an increase in local diversity, a sharp reduction in between-community diversity, and a moderate decline in regional diversity (Fig. 1a–d). Further increasing dispersal ( $\mu, \sigma \approx 5$ ,

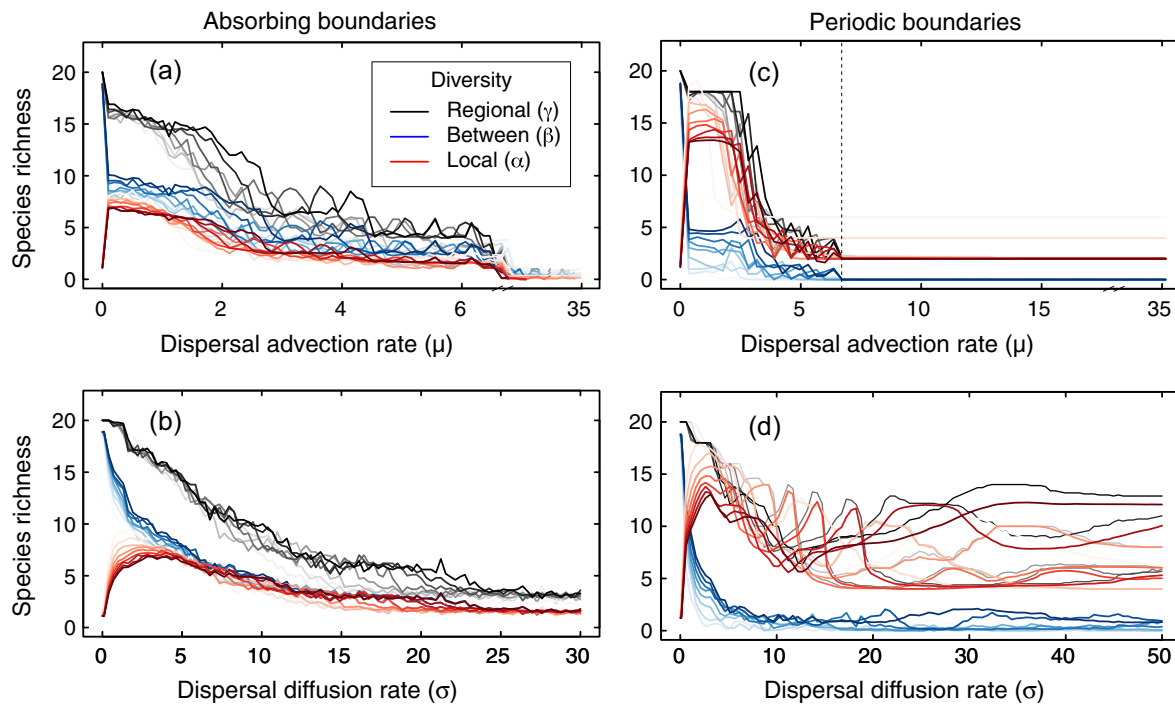


Fig. 1. Metacommunity species richness at multiple spatial scales as a function of dispersal advection (a) and diffusion (b) for different environmental gradients. Red, blue, and black lines depict local ( $\alpha$ ), between-community ( $\beta$ ), and regional diversity ( $\gamma$ ), respectively. In addition to the color (red, blue, black), the translucence of each line represents the strength (slope) of the environmental gradient, which ranges from low (lighter hues) to high (darker hues). Results represent means from 10 replicate simulations. The vertical dashed line in panel (a) depicts when advection rates are high enough to prevent self-recruitment ( $\mu > 2\sigma \approx 5$ ).

30) spatially homogenizes the metacommunity, destroys all spatial rescue effects, and reduces diversity at all scales as regionally dominant species are able to competitively exclude most species across the metacommunity (Fig. 1a–d).

For advective dispersal, local diversity is thus maximized at intermediate rates when advection is high enough to promote spatial rescue effects but not so high as to prevent self-recruitment. Indeed, high advective dispersal rates will spatially couple distant sites experiencing different parts of the environmental gradient, so a species growing in a site characterized by good environmental conditions will receive relatively few recruits from unproductive sites experiencing poor environmental conditions. Hence, even if the vast majority of these arriving recruits survive, abundance at the site experiencing good environmental conditions will be relatively low since the supply rate will be limited. Conversely, a site characterized by poor environmental conditions

might receive a large supply of recruits from sites experiencing good environmental conditions, but because most of those recruits will not survive, local species abundance will also be low.

Diffusive dispersal promotes higher overall levels of species diversity by maintaining the local positive feedback between abundance and recruitment as the dispersal kernel remains centered on the natal site. Hence, self-recruitment can allow species in sites experiencing good environmental conditions to establish larger populations and subsequently subsidize populations at sites experiencing poor environmental conditions via source–sink dynamics (Pulliam 1988). At higher dispersal rates, these mass effects allow for increased abundances for species in non-optimal environments. While these patterns hold regardless of the strength of the environmental gradient (Fig. 1a–d), differences in the diversity–dispersal relationship emerge in metacommunities with absorbing vs. periodic boundary conditions (Fig. 1a, b vs. c, d).

Diversity levels are generally higher under periodic than absorbing boundary conditions because under the latter, all species experience an effective reduction in their recruitment rates as propagules are lost from the metacommunity (Fig. 1). This is particularly true when increasing advective versus diffusive dispersal, which increases the rate at which propagules are whisked away from the metacommunity (Fig. 1a, c vs. Fig. 1b, d). Regional diversity is driven by between-community diversity ( $\beta$ ) at low dispersal in metacommunities with absorbing boundary conditions, as spatial rescue effects allow most species in the metacommunity to persist. Intermediate rates of advection (Fig. 1a, b;  $\mu$ ,  $\sigma = 6, 10$ ) reduce regional species diversity by replacing the local positive feedback between abundance and self-recruitment in closed communities with a regional negative feedback

that allows the same set of regionally dominant species (species with higher regional-scale realized recruitment rate  $F$ ) to monopolize the metacommunity regardless of local environmental conditions. In doing so, advection shifts control of regional diversity ( $\gamma$ ) from between-community ( $\beta$ ) to local ( $\alpha$ ) diversity. Additionally, the negative regional feedback generates relatively uniform abundances for the few regionally dominant species across the entire range of dispersal advection (Fig. 2a;  $\mu > 5$ ).

Initially, similar trends appear in metacommunities characterized by periodic boundary conditions (Fig. 2c, d). Low levels of diffusive dispersal promote spatial rescue effects and spatially homogenize the metacommunity, thus allowing local diversity ( $\alpha$ ) rather than between-community diversity ( $\beta$ ) to dictate regional diversity ( $\gamma$ ).

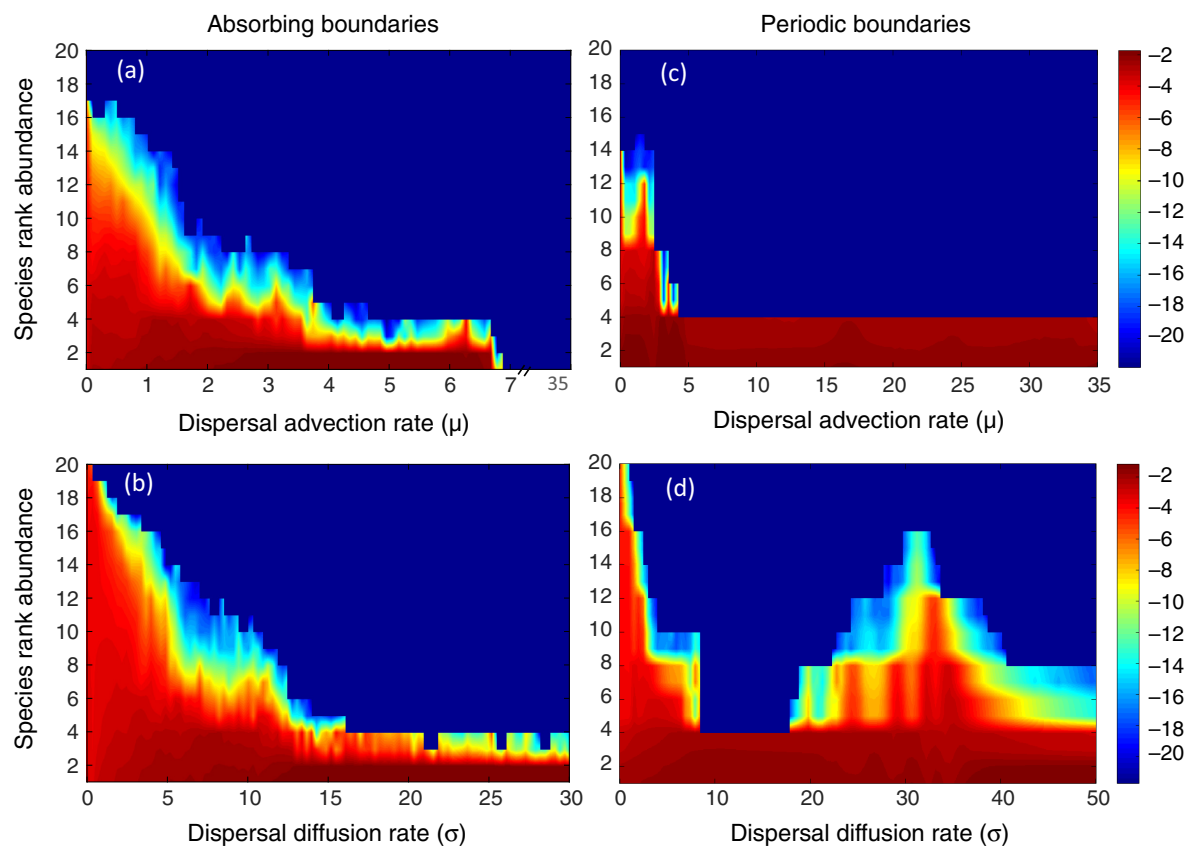


Fig. 2. Species rank abundance as a function of dispersal advection rate (a) and diffusion rate (b). The regional mean abundance of each species is plotted on a log scale as a function of species rank abundance. Color represents log abundance, which ranges from low (cool colors) to high (warm colors). Results represent means from 10 replicate simulations.



Intermediate rates of diffusive dispersal fully spatially homogenize the metacommunity, thus promoting competitive exclusion. Interestingly, further increasing diffusion leads to an additional peak in both local and regional diversity ( $\sigma \sim 10\text{--}30$ , depending on environmental gradient). Here, species are able to persist in more locations throughout the metacommunity due to an environmental rescue effect whereby a portion of the propagules produced in optimal natal sites arrive in equivalently optimal sites far from their origin. This secondary match between a species' physiological optima and the local environment creates a boost in fitness resulting in the resurgence of rare species (Fig. 2d). Hence, the primary peak in species diversity due to spatial rescue and the secondary peak in species diversity due to environmental rescue yield fundamentally different patterns of community structure, with the former being characterized by a more uniform species abundance distribution (many abundant species) and the latter a skewed species abundance distribution (many rare species; Fig. 2d).

This environmental rescue occurs at diffusion rates where dispersal is strong enough to dampen spatial rescue effects, but not strong enough to homogenize the whole system; thus, a secondary peak in diversity exists for all environmental gradients. For weaker gradients (slopes of 0.02–0.05), the secondary peaks in local and regional diversity emerge at lower levels of diffusion because it is easier for dispersal to spatially homogenize a system that is less environmentally heterogeneous (Fig. 1d). Hence, we expect that the second peak should shift to the left (to lower diffusion rates) with decreasing environmental variation slopes (i.e., weaker environmental gradients). Conversely, increasing the slope of the environment leads to the occurrence of an increasingly distinct secondary peak at higher diffusion rates.

#### *Patterns of metacommunity structure*

We applied variation partitioning to the model output in order to determine how different levels of dispersal advection and diffusion affect the ecological interpretation of the spatial and environmental fractions in metacommunities with either absorbing or periodic boundary conditions. In environments characterized by either absorbing and periodic boundary conditions,

increasing the advection ( $\mu$ ) or the diffusion ( $\sigma$ ) rate ultimately decreases the spatial fraction by allowing species to increasingly find and monopolize the sites characterized by their optimal environmental conditions (Fig. 3). Regardless of the nature of dispersal or the boundary conditions, the introduction of dispersal promotes spatial rescue effects that erode the relationship between the environment and community structure, resulting in a spatial fraction explaining as much as 90% of the total variation in community structure. Despite these general similarities, there are key differences in the effect of increased dispersal on the spatial fraction that depend on the boundary conditions and the nature of dispersal.

For absorbing boundary conditions, increasing either aspect of dispersal (advection or diffusion) beyond the levels required for spatial rescue generally promotes species sorting which, in effect, reduces the spatial fraction. However, as previously stated, a few regionally dominant species dominate regardless of environmental conditions, so the spatial fraction never explains <40% of the total variation in community structure regardless of the extent of dispersal (Fig. 3c, f).

Conversely, under periodic boundary conditions, increasing advection versus diffusion has different effects on the sign and the magnitude of the change in the spatial fraction. The most discernible difference between the advection and diffusion appears at low levels of dispersal (Fig. 3i vs. l;  $0 < \mu, \sigma < 8$ ). Initially, increasing the dispersal advection rate increases the spatial fraction, with space explaining anywhere from 40% to 100% of the variation in community structure, whereas increasing the diffusion rate causes a reduction in the variation explained by the spatial fraction from 80 to <10% depending on strength of the gradient. Increasing the dispersal advection rate creates a spatial lag between local environmental conditions and their effects on recruitment and community structure. This spatial lag disrupts the local positive feedback between abundance and self-recruitment, replacing it with a regional negative feedback that erodes the correlation between environmental conditions and community structure and thus increases the spatial fraction (Fig. 3i). Apart from the initial increase under advective dispersal, the predominant trend is a reduction in the spatial fraction. This decrease begins at intermediate

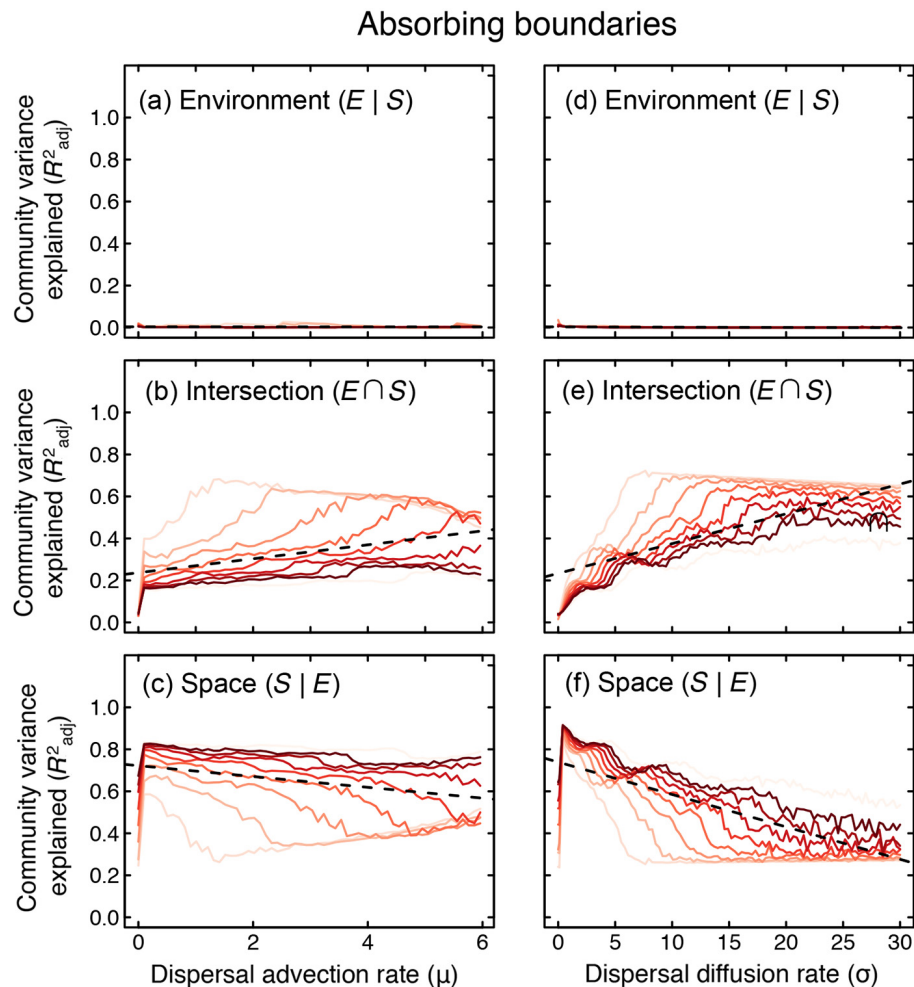


Fig. 3. Variation partitioning of community structure as a function of dispersal advection rate (a–c) and diffusion rate (d–f). Community structure was partitioned into three fractions: the environment ( $E|S$ ), space ( $S|E$ ), and their joint influence or intersection ( $E \cap S$ ) (i.e., the fraction of the variation in community structure jointly influenced by space and the environment). Line color and translucence represent the strength (slope) of the environmental gradient, which ranges from low (lighter hues) to high (darker hues). Results represent means from 10 replicate simulations.

dispersal rates ( $\mu > 8$ ), which lead to spatial homogenization and the loss of spatial rescue effects. The spatial fraction remains high relative to the spatial fraction observed under diffusive dispersal because species are less able to exploit the periodicity of the environment and do not experience environmental rescue, resulting in the presence of a few regionally dominant species, as in absorbing conditions.

Under diffusive dispersal, the initial decrease in the spatial fraction is a consequence of high species sorting, where species are able to reach

their environmental niche and exclude their inferior competitors locally (Fig. 3f). As the diffusion rate increases, environmental rescue increases the degree to which species are able to persist at (multiple) optimal locations, effectively increasing the variation explained by the environment and further reducing the spatial fraction. Overall, these results demonstrate that altering the rates of advective vs. diffusive dispersal can lead to very different patterns of spatial variation in community structure under periodic boundary conditions.

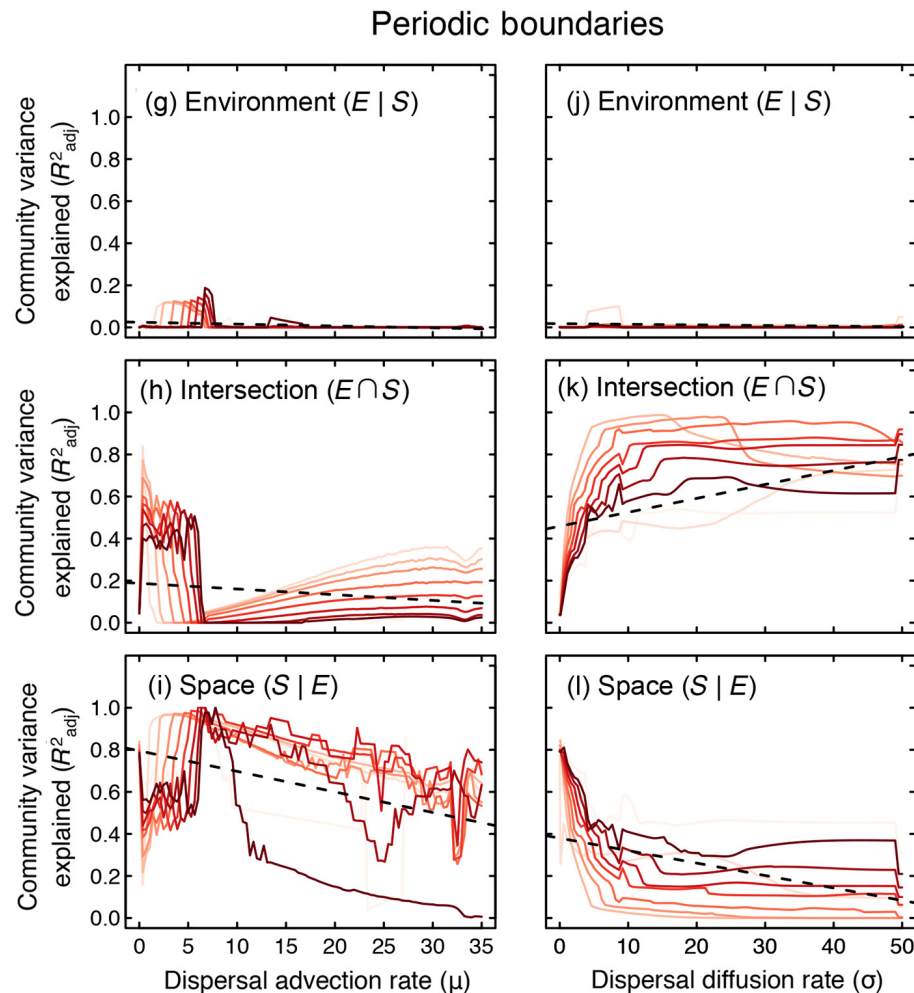


Fig. 3. (Continued)

### Empirical case study

To test our model predictions, we applied variation partitioning to a dataset containing abundances of rocky intertidal species in the high, mid, and low zone along the West Coast of the United States. Species were grouped based on their pelagic larval duration (PLD), which served as a proxy for dispersal ability (Shanks et al. 2003, Shanks 2009, Selkoe and Toonen 2011). This case study shows that the spatial fraction can map to different PLD values (Fig. 4). Indeed, we found no relationship between the spatial fraction and the community's mean group PLD (ANOVA;  $df = 3$ ,  $F = 2.498$ ,  $P\text{-value} = 0.07518$ ; Table 1, Fig. 4) and a significant interaction between PLD and zone (ANOVA;  $df = 6$ ,

$F = 4.408$ ,  $P\text{-value} = 0.00194$ ; Table 1). Hence, the relationship between PLD and the spatial fraction depends on zone. For instance, large spatial fractions were associated with high PLD in the low zone but low PLD in the high zone (Fig. 4). This means that the size of the spatial fraction alone is not a reliable predictor of the extent of dispersal. Additionally, there was a significant relationship between the spatial fraction and zone (ANOVA;  $df = 2$ ,  $F = 14.933$ ,  $P\text{-value} < 0.0001$ ; Table 1). Furthermore, PLD explained a smaller proportion of the variance in the spatial fraction than zone ( $\eta^2 = 0.075$  vs.  $\eta^2 = 0.299$ ; Table 1). This suggests that there are other factors affecting the size of the spatial fraction beyond dispersal (e.g., differences in

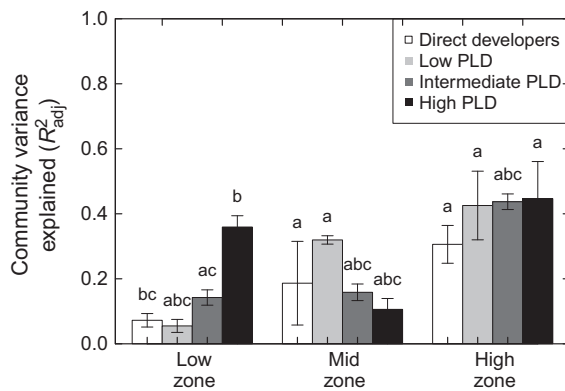


Fig. 4. Variation partitioning results for an intertidal metacommunity. Community structure was partitioned into three fractions: the environment ( $E|S$ ), space ( $S|E$ ), and their joint influence or intersection ( $ENS$ ). The spatial fraction is plotted as a function of intertidal zone (low, mid, high). The color of the bar (white, light gray, dark gray, black) indicates mean group pelagic larval durations (PLD), a measure of dispersal ability (direct dispersers, low, medium, high). Overlapping horizontal lines indicate bars that are not statistically different at the  $\alpha = 0.05$  significance level. Analysis was conducted on log10-transformed spatial fractions.

desiccation stress across zones). Overall, these empirical results are consistent with the effects of dispersal predicted by our model: The spatial fraction is not a measure of dispersal alone and should thus not be used as a direct proxy. Instead, one needs to account for the strength and nature of environmental forcing as well as the type of dispersal in order to correctly interpret the size of the spatial fraction.

## DISCUSSION

Our empirical and theoretical results indicate that the effects of dispersal on patterns of species diversity and abundance cannot easily be determined by applying statistical variation partitioning to observational data collected across multiple scales. Indeed, although increasing dispersal consistently leads to a reduction in the spatial fraction, as predicted by theory, this signature trend is unlikely to be detected from statistical snapshots of observational data because the size of the spatial fraction depends on the

Table 1. Summary of ANOVA model testing the effects of mean group pelagic larval duration (PLD) and zone on the spatial fraction obtained via variation partitioning.

Source	df	MS	F	P-value	Effect size ( $\eta^2$ )
Mean PLD	3	0.2167	2.498	0.07518	0.075
Zone	2	1.2954	14.933	1.89e-05	0.299
Mean PLD $\times$ zone	6	0.3824	4.408	0.00194	0.265
Residuals	36	0.0868			0.361

Note: Analysis was conducted on log10-transformed spatial fractions.

complex interaction between environmental heterogeneity, boundary conditions, and dispersal. Our results have important implications for managing complex and interconnected ecosystems experiencing environmental variability.

### Effects of dispersal on biodiversity across scales

The effects of dispersal on community stability (Holland and Hastings 2008, Gouhier et al. 2010a, b), persistence (Huffaker 1958, Blasius et al. 1999), and biodiversity (Brown and Kodric-Brown 1977, Tilman 1994) have been well established in theory and practice (reviewed by Briggs and Hoopes 2004, Holyoak et al. 2005). When dispersal is too low, environmentally heterogeneous communities become dominated by the strongest local competitors, thus generating low local ( $\alpha$ ) diversity and high between-community ( $\beta$ ) diversity. This type of species sorting is typically associated with low community stability and persistence because each species is rare at the regional scale and thus vulnerable to the loss of the few locations where they are found. Intermediate levels of dispersal promote both species coexistence and community stability by allowing source-sink dynamics to emerge across the metacommunity (Mouquet and Loreau 2003, Gouhier et al. 2010a, b). Under this scenario, the increased movement of organisms leads to high local diversity and low between-community diversity. Overall, these types of spatial rescue effects will arise as long as dispersal is not high enough to fully synchronize the dynamics of all communities. If dispersal is too high, the entire metacommunity behaves like a single, well-mixed community with low local diversity due to



competitive exclusion by the regionally dominant species, zero between-community diversity, and low stability (Mouquet and Loreau 2003a, Gouhier et al. 2010a, b).

Our results based on manipulating dispersal diffusion rates are largely consistent with these predictions. Increasing diffusion initially leads to high local diversity and lower between-community diversity due to source–sink dynamics (Fig. 1b, d). Further increasing diffusion leads to spatial homogenization and species sorting, with low local, between-community, and regional diversity (Fig. 1b, d). However, when environmental conditions are periodic in nature, increasing diffusion even further leads to an unexpected spike of local and regional diversity by (Fig. 1d) due to environmental rescue effects. High levels of dispersal open up the opportunity for species to reach a secondary optimal location, promoting the persistence and subsequent resurgence of rare species, thereby promoting both local and regional diversity. Ultimately, very high diffusion leads to spatial homogenization and low local, between-community, and regional diversity (Fig. 1d).

This dispersal-induced bimodal diversity pattern in periodic environments, which is robust to (1) the strength of the environmental gradient (Fig. 1d) and (2) the addition of environmental stochasticity (Appendix S2), differs from the unimodal predictions based on classical theory (Mouquet and Loreau 2003a). The difference is likely due to the use of a spatially implicit approach by Mouquet and Loreau (2003) whereby dispersing propagules were redistributed uniformly across the metacommunity. Hence, although they were able to manipulate the degree of mixing by altering the dispersal rate, the scale of mixing remained constant and global. In our spatially explicit framework, however, varying the diffusion rate and boundary conditions alters the degree and the scale of mixing by changing the breadth of the dispersal kernel and the linearity of the environmental gradient. We suggest that our results stem from the simultaneous effect of the diffusion rate on the degree of self-recruitment, the scale of dispersal, and the size of the metacommunity. Our advection results further reinforce the notion that some degree of self-recruitment is necessary to generate the spatial rescue effects described by classical theory. We showed a uniform reduction

in local, between-community, and regional diversity when dispersal advection was sufficiently large to disrupt self-recruitment (Fig. 1a). Here, by replacing the local positive feedback between abundance and self-recruitment with a regional negative feedback, advection essentially reduces the fitness of all species, thus resulting in all communities becoming populated by the same few regional dominants. These patterns are expected to hold as long as the advection-to-diffusion ratio is sufficiently high so as to prevent self-recruitment (Appendix S3). Overall, our results suggest that species diversity across scales and the relative influence of local vs. regional processes depend on the complex interplay between the size of the metacommunity, the degree of self-recruitment, and spatial extent of dispersal in environmentally forced metacommunities.

#### *Detecting the effects of dispersal in the real world*

The impracticality of conducting manipulative experiments at the scales needed to document the effects of dispersal on biodiversity has prompted much interest in the development of statistical variation partitioning methods to decompose metacommunity structure into its spatial and environmental fractions (Borcard et al. 1992, 2004, Dray et al. 2006, Peres-Neto et al. 2006). According to these variation partition frameworks, the environmental fraction will be large if dispersal is high enough to allow species to reach their environmental niche and exclude their competitors at local scales (species sorting), whereas the spatial fraction will be large if dispersal is low enough to allow spatial rescue effects without promoting local competitive exclusion (mass effect). Hence, the spatial fraction should be proportional to the degree of dispersal limitation in the metacommunity. Although such variation partitioning methods are increasingly being applied to empirical datasets in order to determine the relative influence of environmental heterogeneity and dispersal on (meta)-community structure in nature, the interpretation of the spatial fraction remains controversial (Gilbert and Bennett 2010, Tuomisto et al. 2012). For example, using simulated data, Gilbert and Bennett (2010) showed that variation partitioning methods were unable to correctly identify the relative importance of dispersal and environmental heterogeneity. However, their tests of variation partitioning methods were based on “model-free”

simulated data that did not incorporate the dynamical feedbacks between local competition and regional dispersal over multiple generations.

Here, using a dynamic metacommunity model, we were able to show that dispersal advection and diffusion leave similar yet distinct signatures that can be detected via variation partitioning under certain scenarios. Our results extend and support the classical ecological interpretation of the spatial fraction by showing that increasing advective or diffusive dispersal ultimately reduces the size of the spatial fraction under both absorbing and periodic boundary conditions. Although this trend (i.e., the negative correlation between the spatial fraction and dispersal) is clear and consistent across all simulated scenarios, the size of the spatial fraction alone cannot be used to infer the relative importance of dispersal because the former depends on a multitude of factors including the strength of the environmental gradient, the nature of dispersal, and the type of boundary conditions. Our empirical results are consistent with our simulations in that the spatial fraction varies significantly across zones, a proxy for environmental stress, but not across PLD, a proxy for dispersal. Furthermore, the significant interaction between PLD and zone suggests that PLD is not a consistent predictor of the spatial fraction.

Taken together, these results resolve an important discrepancy between theoretical expectations and empirical observations: Although increased dispersal will ultimately reduce the spatial fraction (negative trend) under all scenarios, as predicted by theory, detecting this elusive signal in nature is likely to be fraught with difficulties due to the fact that observational studies provide snapshots of the spatial fraction rather than trends and the former are influenced not only by dispersal, but also by the strength of the environmental gradient and the nature of the boundary conditions.

That being said, the more information available about the nature of dispersal and the size of the metacommunity, the more insights can be gleaned about the mechanisms driving the patterns in community structure. In finite-size metacommunities (simulated via absorbing boundaries and a linear environment), the spatial fraction explains more than 40% of the variation in community structure, suggesting that spatial rescue effects are driving coexistence patterns and diversity levels. The added mortality associated with finite

boundaries (propagules are leaving the system) mitigates the differential impact of advective vs. diffusive dispersal on spatial community structure. Conversely, in infinite-size metacommunities (simulated via periodic boundaries and a periodic environment), species do not have to contend with added propagule loss, so the nature of dispersal plays a much larger role. Here, a higher degree of self-recruitment can bolster the ability of species to thrive locally and persist at the regional level. Thus, the mechanisms driving the magnitude of the spatial fraction in periodic environments are the increased availability of suitable environmental conditions and the high degree of self-recruitment due to diffusive dispersal which, when combined, enable rare species to persist across the metacommunity via both spatial and environmental rescue. Overall, our results suggest that although variation partitioning methods could, in theory, be used to tease apart the relative importance of environmental heterogeneity and dispersal on community structure, their direct applicability in the real world is likely to be limited. Hence, while a negative relationship between dispersal and the spatial fraction may be an indicator of increased connectivity in metacommunities, the size of the spatial fraction alone is not sufficient to determine the extent of connectivity in natural systems. Consequently, our results highlight the mistakes likely to be made when attempting to infer ecological mechanisms from statistical snapshots of natural metacommunities via variation partitioning.

### *Spatial management implications*

Metapopulation theory has long been used to inform conservation and management decisions because of its ability to account for the effects of local and regional processes on the persistence of species across scales (reviewed by Hanski 1998). Indeed, metapopulation theory is largely responsible for identifying the role of connectivity in maintaining local populations. Although promoting connectivity has become a key objective in the spatial management of interconnected ecosystems (Botsford et al. 2001, 2003), too much connectivity can be detrimental to persistence by synchronizing and destabilizing the dynamics of metacommunities (Gouhier et al. 2010a, 2013). Hence, determining when connectivity will promote or reduce persistence is critical in order to

effectively manage and conserve natural ecosystems (Earn et al. 2000).

Our results suggest exercising caution when attempting to evaluate the extent of connectivity in a metacommunity via variation partitioning. Indeed, a small spatial fraction can emerge for either low or high rates of advective or diffusive dispersal under both absorbing and periodic boundary conditions. Hence, the size of the spatial fraction alone is not sufficient to infer the extent of dispersal or connectivity in metacommunities. We suggest that applying variation partitioning to system-specific dynamical models parameterized with real data can help improve our ability to understand and manage natural systems by mapping statistical patterns in metacommunity structure to their underlying ecological processes.

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