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LETTER

General relationships between consumer dispersal, resource dispersal and metacommunity diversity

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Abstract

One of the central questions of metacommunity theory is how dispersal of organisms affects species diversity. Here, we show that the diversity–dispersal relationship should not be studied in isolation of other abiotic and biotic flows in the metacommunity. We study a mechanistic metacommunity model in which consumer species compete for an abiotic or biotic resource. We consider both consumer species specialised to a habitat patch, and generalist species capable of using the resource throughout the metacommunity. We present analytical results for different limiting values of consumer dispersal and resource dispersal, and complement these results with simulations for intermediate dispersal values. Our analysis reveals generic patterns for the combined effects of consumer and resource dispersal on the metacommunity diversity of consumer species, and shows that hump-shaped relationships between local diversity and dispersal are not universal. Diversity–dispersal relationships can also be monotonically increasing or multimodal. Our work is a new step towards a general theory of metacommunity diversity integrating dispersal at multiple trophic levels.

Keywords

Community ecology, dispersal, diversity-dispersal relationship, ecosystem ecology, habitat generalist, habitat specialist, limited resource access, metacommunity, meta-ecosystem, resource competition.

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INTRODUCTION

Ecological communities are governed by processes at various spatial scales (MacArthur & Wilson 1967; Ricklefs 1987; Levin 1992). One of the tools to study spatial scales in ecology is the metacommunity concept (Leibold *et al*. 2004; Holyoak *et al*. 2005). A metacommunity is a set of communities in a patchy habitat; communities in different patches are connected by dispersal (or, synonymously, by migration). Metacommunity models allow us to study the effect of dispersal on the structure and functioning of communities at the local scale, i.e. at the scale of each community, and at the regional scale, i.e. at the scale of the metacommunity as a whole.

One of the central questions of metacommunity theory is how dispersal affects local and regional diversity. A standard theoretical argument decomposes the diversity–dispersal relationship into three parts (Loreau *et al*. 2003a; Mouquet & Loreau 2003; Leibold *et al*. 2004). First, when dispersal is weak, local communities are essentially isolated. Local diversity is low due to competitive exclusion at the local scale; regional diversity is high due to spatial heterogeneity between patches. Second, for moderate dispersal, species disperse from patches where they thrive to patches where they cannot survive without dispersal. Hence, local diversity increases, while regional diversity remains constant or decreases slowly. This mixing of local communities continues until local and regional diversity are equal. Third, when dispersal is strong, the metacommunity is homogenised and competitive exclusion acts at the regional scale. Both local and regional diversity decrease. In summary, theory predicts a hump-shaped relationship between local diversity and dispersal and a monotonically decreasing relationship between regional diversity and dispersal.

Numerous experimental studies have measured the diversity–dispersal relationship by manipulating dispersal in microbial, plant and animal metacommunities (Logue *et al*. 2011). Cadotte (2006) conducted a meta-analysis of 50 such experiments. He found that local diversity increases with dispersal for weak to moderate dispersal, in agreement with metacommunity theory. However, he obtained ambiguous results for the strong-dispersal part of the diversity–dispersal relationship. Some studies found that local and regional diversity decrease with increasing dispersal, whereas other studies suggest that local and regional diversity are unaffected by dispersal when dispersal is strong (Forbes & Chase 2002; Kneitel & Miller 2003; Howeth & Leibold 2010; Matthiessen *et al*. 2010).

Existing theory considers diversity and dispersal of a group of species in isolation of other spatial flows in the metacommunity. Relaxing this assumption may lead to different predictions, as has been advocated by meta-ecosystem theory (Loreau *et al*. 2003b; Massol *et al*. 2011). In particular, it is commonly assumed that a metacommunity is homogenised when dispersal is strong. But even if the pool of species of which we track diversity is homogeneously distributed, this may not be the case for the entire ecosystem including

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resources and consumers. We hypothesise that dispersal at lower or higher trophic levels affects the diversity–dispersal relationship at the focal trophic level. Here, we build a theory that takes into account this extra layer of complexity, focusing on the effect of dispersal on species diversity.

To do so, we introduce a spatial consumer-resource model. As in existing metacommunity models, we look at a set of interconnected patches in which a resource is consumed locally, and consumers can disperse between patches (Loreau *et al.* 2003a; Loreau 2010). But contrary to existing metacommunity models, we also consider resource dispersal. Furthermore, we establish a connection with the theory of resource access limitation (Huston & DeAngelis 1994; Loreau 1998). The latter theory predicts that resource dispersal intensifies competition between consumer species. Thus, in contrast to previous theories, which have dealt with consumer and resource dispersal separately, we investigate the combined effects of consumer and resource dispersal on metacommunity diversity.

More specifically, we model a single limiting resource that is consumed by a pool of consumer species. The efficiency with which the resource is consumed varies spatially, and differs between species. We focus on competition for the spatially distributed resource between specialist and generalist consumer species. Specialists are able to use the resource efficiently in particular patches. Generalists cannot outcompete specialists in any single local community, but can use the resource throughout the metacommunity. Their resource use averaged over the patches is more efficient than the average resource use of specialist species. We study which dispersal conditions, for both consumers and the resource, favour specialists or generalists.

Thus, we address three questions in this work: (1) how metacommunity diversity depends on consumer and resource dispersal, (2) what diversity–dispersal relationships are expected for spatial resource competition and (3) what dispersal values promote specialist or generalist species. To answer these questions, we first derive analytical results for a number of limiting cases, assuming that consumer and resource dispersal are either very small or very large. We then use numerical simulations to investigate metacommunities for intermediate dispersal values and to describe their generic diversity–dispersal relationships.

SPATIAL CONSUMER-RESOURCE MODEL

We present a mechanistic consumer-resource model to explore the effects of dispersal on species diversity. We consider one limiting resource and several consumer species, all spatially distributed over habitat patches. We assume, as in previous metacommunity models (Loreau & Mouquet 1999; Loreau *et al.* 2003a; Mouquet & Loreau 2003), that resource consumption rates of consumers differ between patches, i.e. that their growth rates depend on local environmental conditions, such as temperature, acidity or the presence of a natural enemy. Competition between consumer species is determined by their patch-dependent resource consumption rates.

We denote by M the number of habitat patches in the metacommunity, and by S the number of consumer species competing for the resource. The dynamical variables of the model are the biomass of consumer species i in patch k, denoted by N_{ik}, and the amount of resource in patch k, denoted by R_k. The dynamical equations are

$$\begin{aligned}\frac{\mathrm{d}N_{ik}}{\mathrm{d}t} &= ec_{ik}R_kN_{ik} - mN_{ik} + \alpha(\langle N_i\rangle - N_{ik})\\ \frac{\mathrm{d}R_k}{\mathrm{d}t} &= g_k(R_k) - \sum_i c_{ik}R_kN_{ik} + \beta(\langle R\rangle - R_k).\end{aligned} \tag{1}$$

The brackets in $\langle N_i\rangle$ and $\langle R\rangle$ stand for the average over patches, i.e. $\langle N_i\rangle = \frac{1}{M}\sum_k N_{ik}$ and $\langle R\rangle = \frac{1}{M}\sum_k R_k$.

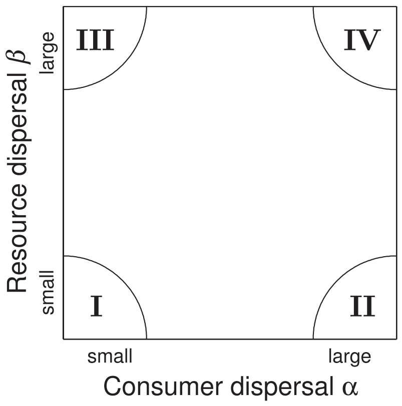
Species i in patch k consumes the resource at rate c_{ik}, converts it to new biomass with efficiency e and dies at rate m. For simplicity, and following Loreau *et al.* (2003a), we assume that efficiency e and mortality rate m are patch- and species independent. The resource in patch k changes at rate $g_k(R_k)$, with

$$\begin{aligned}&g_k(R_k) = a(A_k - R_k) \qquad \text{for an abiotic resource,}\\ &g_k(R_k) = bR_k(B_k - R_k) \quad \text{for a biotic resource.}\end{aligned}$$

In the case of an abiotic resource, the resource in patch k is supplied at rate aA_k and lost at rate a. In the case of a biotic resource, the resource in patch k has intrinsic growth rate bB_k and carrying capacity B_k. Parameters A_k and B_k can be interpreted as patch fertilities. If patch k is empty (no consumers) and isolated (no dispersal), the equilibrium amount of resource is equal to A_k or B_k. We assume that patch fertilities differ between patches.

Consumer species disperse between patches at rate α and the resource disperses (i.e. migrates) between patches at rate β. As in previous metacommunity models (Loreau & Mouquet 1999; Loreau *et al.* 2003a; Mouquet & Loreau 2003), we model the dispersal process in a minimal way: dispersal is assumed to be patch-, species- and density independent. These simplifying assumptions allow us to focus on the general effects of consumer and resource dispersal. Consumer dispersal can be much larger than resource dispersal (e.g. plants competing for a soil nutrient such as phosphorus), of the same order of magnitude (e.g. zooplankton species competing for phytoplankton, both undergoing passive dispersal) or much smaller (e.g. bacteria trapped in a biofilm competing for a freely flowing nutrient). In habitats without specific barriers to dispersal, however, consumers are typically more mobile than resources (McCann *et al.* 2005).

We are interested in the equilibrium composition of the metacommunity. It can be shown that in a metacommunity with M patches at most M species can persist (see Appendix S1). We investigate how the equilibrium metacommunity composition depends on the model parameters. In particular, we formulate our results in terms of specialist and generalist consumers. A consumer species specialised on patch k has large consumption rate c_{ik}. A generalist consumer species has large average consumption rate $\langle c_i\rangle = \frac{1}{M}\sum_k c_{ik}$. No species is expected to be specialised on a large number of patches, or to be simultaneously a good specialist and a good generalist.



I Isolated local communities
→ Each local community is dominated
by best specialist consumer

II Regional consumers, M local resources
→ At most M consumers coexist regionally
(specialists and/or generalists)

III Local consumers, one regional resource
→ One patch is dominated by the overall
best specialist consumer; other patches
are (almost) empty of consumers

IV Homogeneous metacommunity
→ The metacommunity is dominated
by best generalist consumer

Figure 1 Four limiting cases of consumer and resource dispersal, and the resulting metacommunity structure. Consumer dispersal α and resource dispersal β affect the competition between consumer species for a spatially distributed resource. We analyse four limiting cases: (I) both α and β small; (II) α large and β small; (III) α small and β large; (IV) both α and β large. These limiting cases provide four reference points for the relationship between dispersal and metacommunity diversity. They are extended to intermediate dispersal values in Figs 2 and 3.

We assume that the consumer species' consumption rates are subject to specialist-generalist trade-offs (Kneitel & Chase 2004).

FOUR LIMITING CASES

Model (1) describes a pool of S consumer species competing for a single limiting resource distributed over M patches. We are interested in how the equilibrium metacommunity composition depends on consumer dispersal α and resource dispersal β. It is difficult (if not impossible) to study model (1) analytically for arbitrary dispersal values α and β. However, it is possible to obtain analytical results by assuming that consumer dispersal and resource dispersal are either very small or very large. In this section, we define and investigate four limiting cases for dispersal values α and β. The predictions of the limiting cases are useful to understand the model behaviour for arbitrary dispersal values α and β, as we show in the next section.

The four limiting cases are represented schematically in Fig. 1:

- When both α and β are small (case I), local communities are isolated. In each local community S consumer species compete for the resource. No species persists if patch fertility is too small (see Appendix S4 for mathematical details). If patch fertility is sufficiently large, the species that uses the resource most efficiently excludes the other $S - 1$ species. That is, the consumer species that is most specialised on the resource in the patch wins the local competition. Local diversity is small, but regional diversity is typically large, because the most efficient consumer species differ between patches. Several specialist species coexist at the regional scale.
- When α is large and β is small (case II), patches are permeable from the viewpoint of the consumers, but are isolated from the viewpoint of the resource. Hence, consumers compete regionally for the locally isolated resource. The resource bound to each of the M local communities corresponds effectively to M distinct resources. Indeed, in the limit $\alpha\to\infty$ and $\beta = 0$ model (1) reduces to a model of S species competing for M resources (see Appendix S2),

$$\begin{aligned}\frac{\mathrm{d}\langle N_i\rangle}{\mathrm{d}t} &= e\sum_k \frac{c_{ik}}{M}R_k\langle N_i\rangle - m\langle N_i\rangle\\ \frac{\mathrm{d}R_k}{\mathrm{d}t} &= g_k(R_k) - \sum_i c_{ik}R_k\langle N_i\rangle.\end{aligned} \tag{2}$$

At equilibrium at most M species persist. The set of persisting species depends on the model parameters, and can be determined by applying non-spatial resource competition theory (Tilman 1982; Grover 1997). Local and regional diversity are equal, and can be small or large depending on the outcome of resource competition.

- When α is small and β is large (case III), patches are permeable from the viewpoint of the resource, but are isolated from the viewpoint of the consumers. Hence, locally isolated consumers compete regionally for the resource. A consumer species bound to each of the M local communities corresponds effectively to M distinct consumer populations. Hence, there are MS effective consumer populations in total. Indeed, in this limit model (1) reduces to a model of MS species competing for one resource (see Appendix S2),

$$\begin{aligned}\frac{\mathrm{d}N_{ik}}{\mathrm{d}t} &= ec_{ik}\langle R\rangle N_{ik} - mN_{ik}\\ \frac{\mathrm{d}\langle R\rangle}{\mathrm{d}t} &= G(\langle R\rangle) - \sum_{i,k}\frac{c_{ik}}{M}\langle R\rangle N_{ik}.\end{aligned} \tag{3}$$

with

$$\begin{aligned}G(\langle R\rangle) &= a(\langle A\rangle - \langle R\rangle) &&\text{for an abiotic resource,}\\ G(\langle R\rangle) &= b\langle R\rangle(\langle B\rangle - \langle R\rangle) &&\text{for a biotic resource.}\end{aligned}$$

No species persists if patch fertility is too small (see Appendix S4). If patch fertility is sufficiently large, the consumer population that uses the resource most efficiently excludes all the other populations. That is, at equilibrium only a single patch is occupied, that specific patch is occupied by a single species, and that specific species consumes the regionally homogenised resource. The consumer species that is most specialised on a local resource dominates the entire metacommunity. Local and regional diversity are equal and small.

- When both α and β are large (case IV), the metacommunity is homogenised both from the viewpoint of the consumers and from that of the resource. The spatial structure of the metacommunity dissolves; the S consumer species compete for the resource at the regional scale. The reduced model is (see Appendix S2),

$$\begin{aligned}\frac{\mathrm{d}\langle N_i\rangle}{\mathrm{d}t} &= e\langle c_i\rangle\langle R\rangle\langle N_i\rangle - m\langle N_i\rangle \\ \frac{\mathrm{d}\langle R\rangle}{\mathrm{d}t} &= G(\langle R\rangle) - \sum_i \langle c_i\rangle\langle R\rangle\langle N_i\rangle.\end{aligned} \tag{4}$$

No species persists if patch fertility is too small (see Appendix S4). If patch fertility is sufficiently large, the species that uses the resource most efficiently averaged over spatial heterogeneity excludes the other species. That is, the most efficient generalist species dominates the metacommunity. Local and regional diversity are equal and small.

The analysis of these limiting cases provides four reference points for the relationship between consumer dispersal, resource dispersal and metacommunity diversity. When both consumer dispersal α and resource dispersal β are small, each patch is dominated by a single consumer species and the dominant species differ between patches. When consumer dispersal α is large (and β small), the patch compositions mix and the regional competition for the locally isolated resource can have different outcomes. When resource dispersal β is large (and α small), the species that is most specialised on its patch excludes the other species. When both consumer dispersal α and resource dispersal β are large, the most efficient consumer species averaged over spatial heterogeneity, i.e. the best generalist species, excludes the other species.

DIVERSITY–DISPERSAL RELATIONSHIPS

In the previous section, we have established some reference points for the relationship between consumer dispersal, resource dispersal and metacommunity composition. Here, we present numerical simulations of model (1) to extend the previous results to intermediate dispersal values. First, we study a metacommunity with two patches. Then, we show that larger metacommunities exhibit similar patterns. Finally, we connect our results with the experimentally often measured diversity–dispersal relationship.

To perform numerical simulations, we integrated model (1) numerically over a long time span using the MATLAB solver ode15s (MathWorks, Natick, MA, USA). At the end of each simulation, we checked that an equilibrium was reached [by evaluating the right-hand side of eqn (1)] and that the equilibrium was stable (by computing the eigenvalues of the Jacobian). The simulations suggest that there is a unique stable equilibrium for all parameter values considered in this study.

First, we consider a metacommunity with two patches occupied by two specialist species S1 and S2. The resource is assumed to be biotic. The effects of consumer and resource dispersal on equilibrium metacommunity composition and on local and regional diversity are shown in Figs 2 and 3, rows (a–b). We quantify metacommunity diversity using Shannon diversity, which is more convenient for our purpose than species richness (Appendix S3; Fig. S1). As predicted by the previous section, both species coexist regionally for small α and small β, the best specialist species (here species S1) dominates for small α and large β, the best generalist species (here species S1) dominates for large α and large β, and different scenarios are possible for large α and small β. In Figs 2a and 3a, patch fertilities are sufficiently large for both species to persist. In Figs 2b and 3b, patch fertility B_1 is too small to maintain specialist species S1. The corresponding diversity patterns are similar except for large α and small β [Fig. 3, rows (a–b)].

We then add a generalist species G to the two-species two-patch metacommunity [Figs 2 and 3, rows (c–d)]. The generalist species has no effect on the metacommunity composition for small α. For large α and small β, the metacommunity can have different compositions depending on the patch fertilities. In Figs 2c and 3c, species G excludes the specialist species. In Figs 2d and 3d, species S2 and G coexist locally. For large α and large β, the generalist species G dominates (if patch fertility is sufficiently large). The odds for generalist species G to be present in the metacommunity at equilibrium increase when increasing α, especially for large β. Again, the diversity patterns are similar except for large α and small β [Fig. 3, rows (c–d)].

Next, we investigate the robustness of the above results with respect to the model assumptions. First, we study the dependence of metacommunity composition on patch fertilities (Fig. S2, panel (a) and Fig. S3 for the two-species metacommunities; Fig. S2, panel (b) and Fig. S4 for the three-species metacommunities). The regions of dispersal values α and β for which species can persist, change in accordance with the mechanisms explained above. Second, we study the effect of replacing a biotic resource by an abiotic resource (compare Fig. S5 with Fig. 2 and Fig. S6 with Fig. 3). Taking the same patch fertilities for biotic and abiotic resource, the metacommunity patterns are qualitatively similar.

Third, we investigate whether the results for metacommunities with two patches extend to larger metacommunities. We used different procedures to generate simulation parameters (Appendix S5). A first procedure does not impose a trade-off on the set of consumption rates c_{ik} for species i. A second procedure assumes a linear trade-off, i.e. the sum $\sum_k c_{ik}$ is the same for all species i. A third procedure assumes a quadratic trade-off, i.e. the sum $\sum_k c_{ik}^2$ is the same for all species i. As explained in Appendix S5, only the last procedure implements a specialist-generalist trade-off (Kneitel & Chase 2004). It prevents a species from being specialised on a large number of patches, or from being simultaneously a specialist and a generalist. Nevertheless, we find that the three procedures lead to comparable diversity patterns (Fig. S8), indicating that the patterns we obtained are generic.

Using the parameter generation procedure with a quadratic trade-off, we simulated a large number of metacommunities with $M = 5$ patches and $S = 20$ species. Examples of results for four such metacommunities are shown in Figure S10.

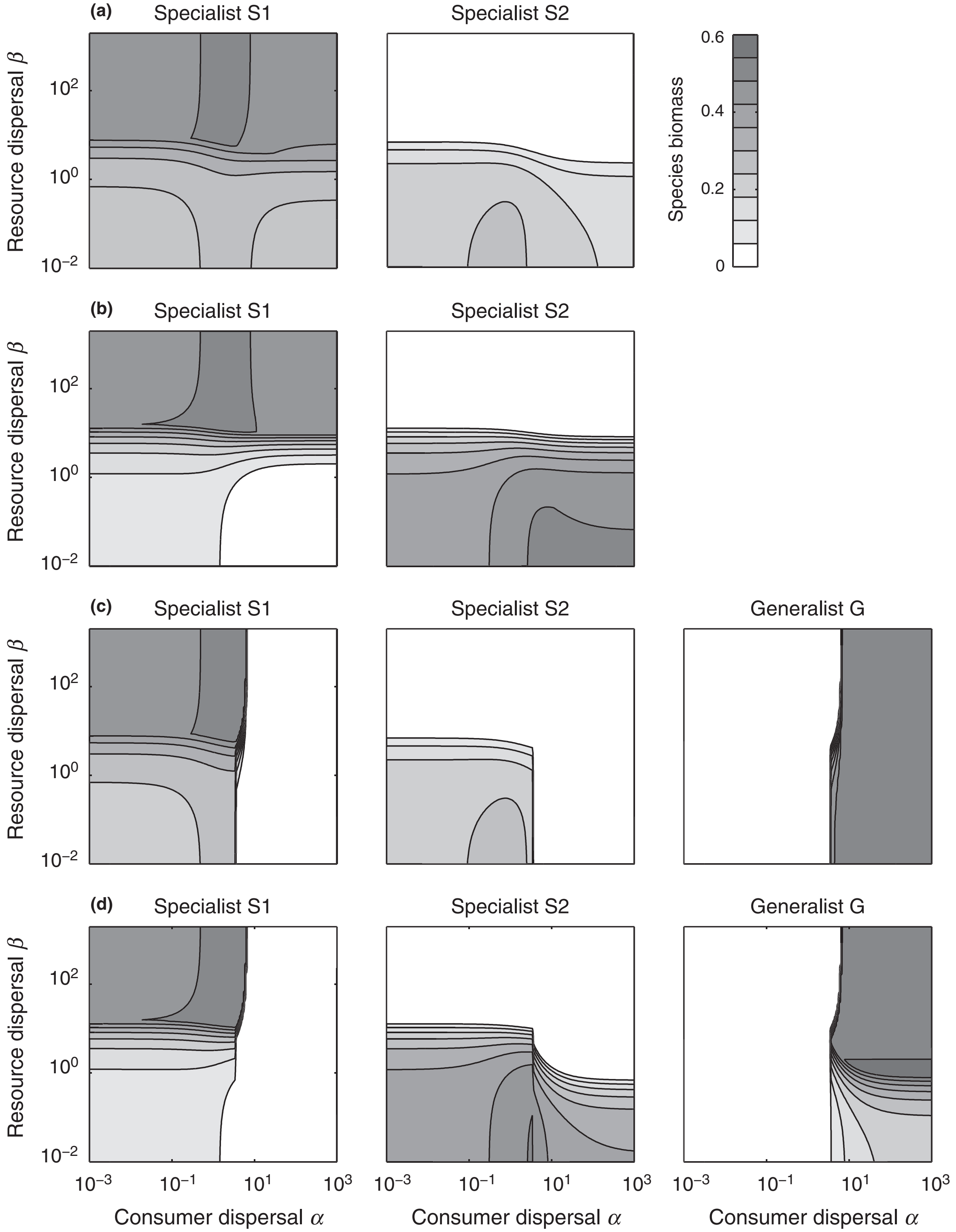


Figure 2. Effects of consumer and resource dispersal on the composition of two-patch metacommunities with a biotic resource. Equilibrium consumer biomass is plotted for four metacommunities. Rows (a–b): metacommunities with two specialist consumer species S1 and S2; patch fertilities differ between rows (a) and (b). Rows (c–d): metacommunities with three consumer species: two specialists S1 and S2 and one generalist G; patch fertilities differ between rows (c) and (d). Parameter values: $e = m = b = 1$. $c_{11} = 3.0$, $c_{12} = 0$ for species S1; $c_{21} = 0$, $c_{22} = 2.6$ for species S2; $c_{31} = 1.8$, $c_{32} = 1.6$ for species G. (a) $B_1 = B_2 = 1.0$; (b) $B_1 = 0.6$, $B_2 = 1.4$; (c) $B_1 = 1.0$, $B_2 = 1.0$; (d) $B_1 = 0.6$, $B_2 = 1.4$.

The metacommunity diversity patterns are similar over a large region of dispersal values. There are qualitative differences between simulations only for large α and small β; the outcomes then range from competitive exclusion to the local coexistence of five species (the maximal number of species that can coexist regionally in a metacommunity with five

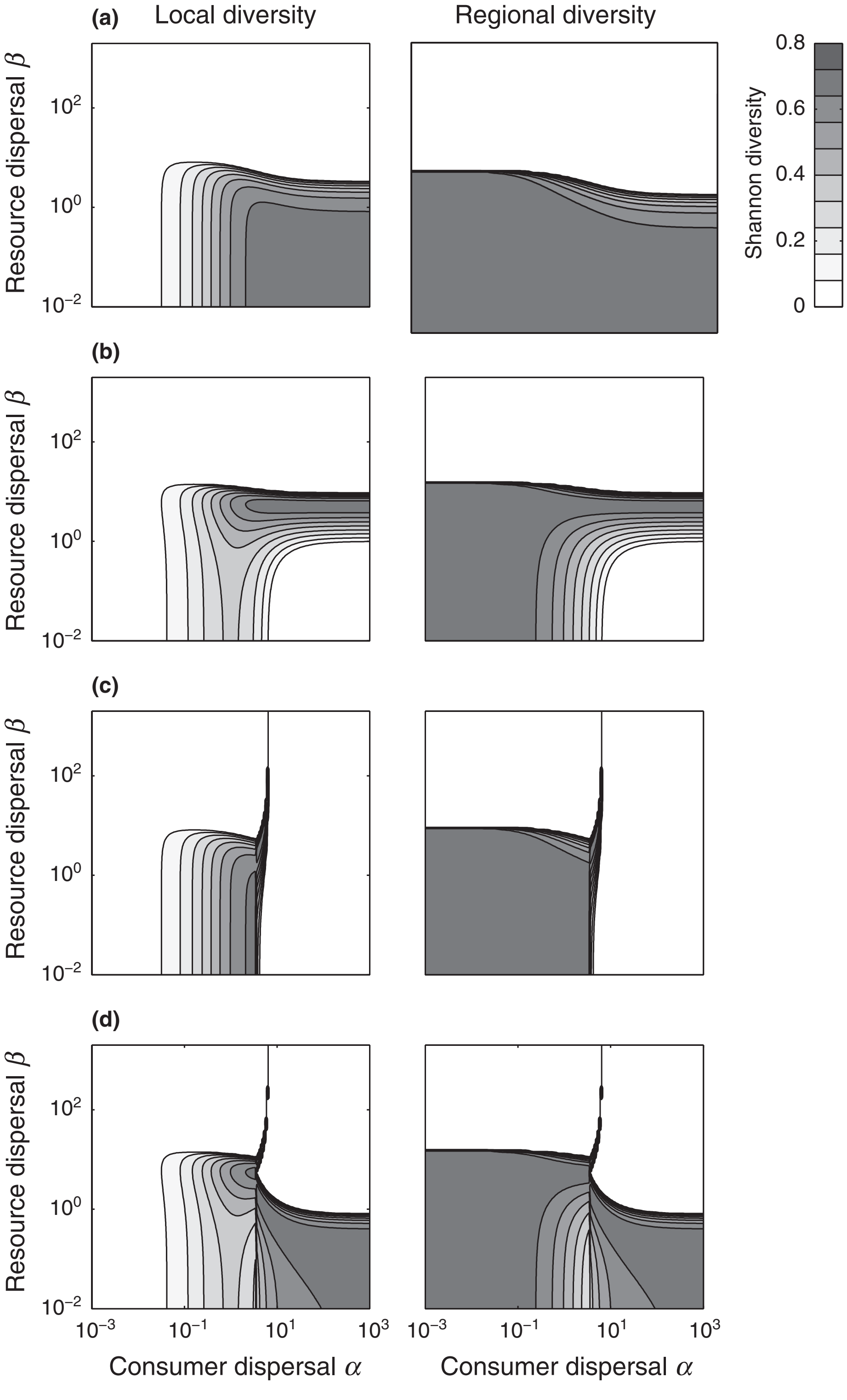


Figure 3. Effects of consumer and resource dispersal on the diversity in two-patch metacommunities with a biotic resource. For the same metacommunities as in Fig. 2 we plot local and regional diversity, measured by Shannon diversity (see Appendix S3). The first two metacommunities [rows (a–b)] consist of two specialist species S1 and S2. The last two metacommunities [rows (c–d)] consist of two specialist species S1 and S2 and one generalist species G.

patches), as predicted by our analysis of the corresponding limiting case in the previous section. The patterns describing the presence of specialist *vs*. generalist consumer species are also similar. Specialists are favoured for small α, especially when β is large; generalists are favoured for large α, especially when β is large. In short, both the diversity patterns and the specialist *vs*. generalist patterns are similar to those for two-patch metacommunities (Figs 2 and 3).

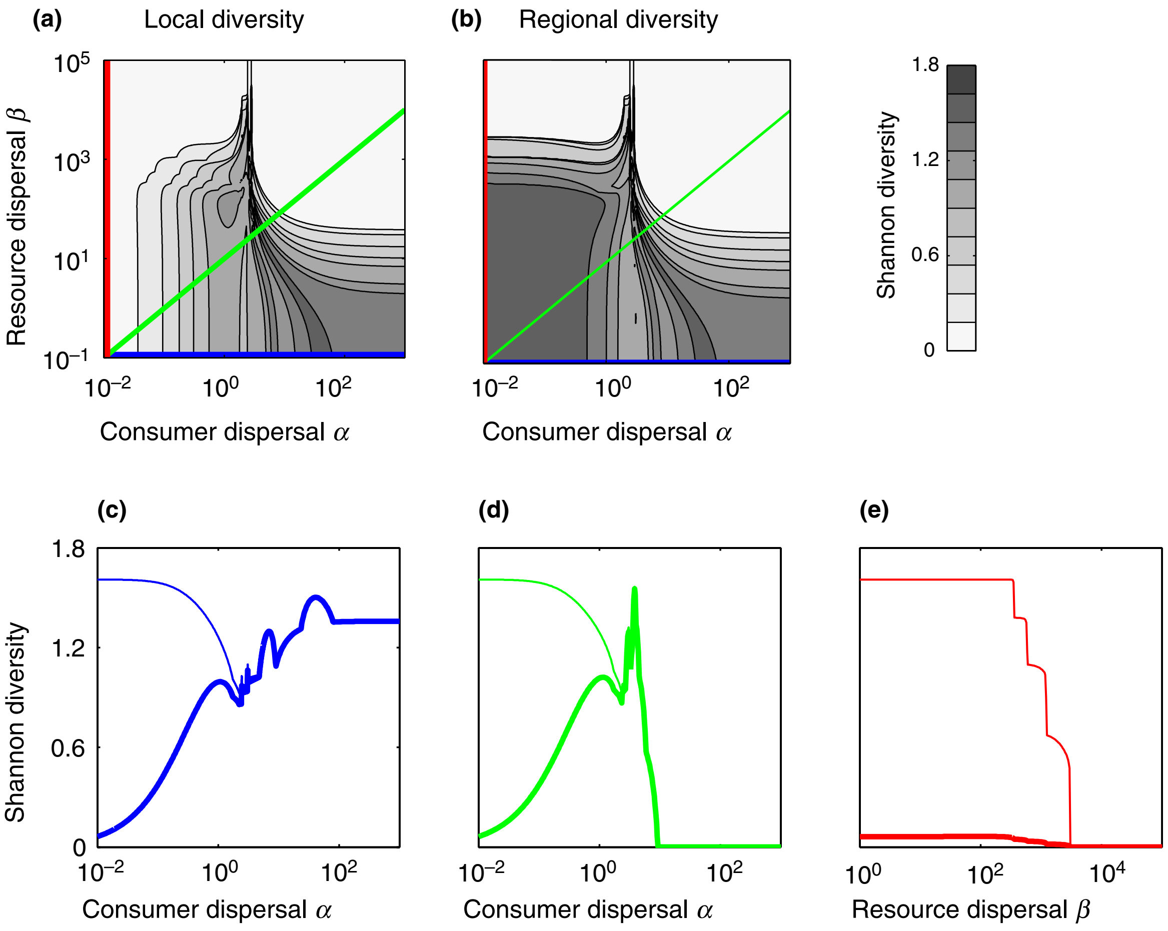


Figure 4. Our model predicts a range of one-dimensional diversity–dispersal relationships. Here, we study a metacommunity with $M = 5$ patches and $S = 20$ species, in which parameters were generated with the procedure described in Appendix S5. Local and regional diversity patterns [panels (a–b)] are qualitatively similar to the patterns for two-patch metacommunities (compare with Fig. 3). From the two-dimensional patterns, we derive three one-dimensional diversity–dispersal relationships. Blue cross section, panel (c): consumer dispersal α varies while keeping resource dispersal β small. Green cross section, panel (d): consumer dispersal α and resource dispersal β vary simultaneously. Red cross section, panel (e): resource dispersal β varies while keeping consumer dispersal α small. Thick line: local diversity; thin line: regional diversity.

Finally, we investigate which diversity–dispersal relationships are predicted by our model. There are several ways to take a one-dimensional cross section of a two-dimensional metacommunity diversity pattern (the two dimensions correspond to consumer dispersal α and resource dispersal β). As an illustration, we construct three diversity–dispersal relationships for a metacommunity with $M = 5$ patches and $S = 20$ species (Fig. 4). For the first relationship, we increase consumer dispersal while keeping resource dispersal small [panel (c)]. Local diversity shows an overall increasing trend despite irregularities; regional diversity decreases towards local diversity until the two diversities coincide. For the second relationship, we increase consumer dispersal and resource dispersal simultaneously [panel (d)]. Local diversity shows a hump-shaped pattern; regional diversity decreases towards local diversity. For the third relationship, we increase resource dispersal while keeping consumer dispersal small [panel (e)]. Local diversity is small for all dispersal values; regional diversity decreases steeply from maximal diversity to zero diversity.

We checked the robustness of these findings for a large number of metacommunities using the parameter generation procedures without and with trade-offs (Figs S9 and S11). We obtain qualitatively similar diversity–dispersal relationships to those for the example in Fig. 4, except for the last part of the first relationship, when consumer dispersal is strong and further increases while resource dispersal is weak and constant. This part can be slowly increasing, slowly decreasing or steeply decreasing to zero. This observation is consistent with our results for the limiting case of large α and small β, for which different outcomes are possible. In short, our model predicts a wide range of diversity–dispersal relationships.

DISCUSSION

Our metacommunity model generalises previous theories by considering patches that are coupled by both consumer dispersal and resource dispersal. We have shown that both consumer dispersal and resource dispersal strongly affect metacommunity diversity. When considering the effect of resource dispersal, we recover the predictions of models describing limited resource access (Huston & DeAngelis 1994; Loreau 1998). Without dispersal patches are dominated by different consumer species, so that locally dominant consumer species coexist at the regional scale. Increasing resource dispersal homogenises the spatial distribution of the resource and increases resource competition between consumer species, even if competing species occupy different patches. As a result, regional diversity decreases with increasing resource dispersal.

When considering the effect of consumer dispersal, we recover some predictions of previous metacommunity models (Loreau & Mouquet 1999; Mouquet & Loreau 2003). Local communities, which are dissimilar without dispersal, are mixed when increasing consumer dispersal. As a result, consumer species can be maintained in patches in which they cannot persist without dispersal (that is, source-sink effects). The increase in local diversity with consumer dispersal continues until local and regional diversity are equal. When further increasing consumer dispersal, however, different scenarios are possible. It is generally argued that large dispersal homogenises the metacommunity. As the spatial structure no longer provides a mechanism for regional species coexistence, metacommunity diversity should collapse. However, this scenario implicitly assumes that increased consumer dispersal also leads to increased resource dispersal. If this is not the case, that is, if consumer dispersal increases while resource dispersal remains small, consumer species compete for a resource that is isolated in different habitat patches. We have shown that this situation is equivalent to consumer species competing for distinct ‘effective’ resources, that is, resources bound to different patches (Abrams 1988). Therefore, several (up to the number of patches) consumer species can coexist locally with large consumer dispersal. Whether this coexistence is realised depends on the outcome of resource competition between consumer species. For the case of a two-patch metacommunity, the resulting composition can be determined by a graphical analysis, analogous to non-spatial competition for two resources (Tilman 1982; Grover 1997).

Thus, our study extends metacommunity theory and unifies it with limited resource access theory. This unification also provides a broader perspective on the relationship between local diversity and consumer dispersal, which is one of the main patterns predicted by metacommunity theory. Previous models generically predict hump-shaped relationships (Loreau *et al.* 2003a; Mouquet & Loreau 2003). In contrast, our model generically predicts a range of possible relationships. In particular, if consumer dispersal varies but resource dispersal stays constant, the diversity–dispersal relationship changes from hump-shaped to overall increasing (with irregularities, however), depending on the level of metacommunity diversity for large consumer dispersal and small resource dispersal. Hence, hump-shaped diversity–dispersal relationships cannot be expected to hold universally. However, our model does predict hump-shaped relationships if increasing consumer dispersal entails a concomitant increase in resource dispersal. Mouquet & Loreau (2003) considered also a non-generic set of parameters for which all species have exactly the same competitive ability at the regional scale, leading to a monotonically increasing relationship.

Our model includes previous predictions of metacommunity theory for the diversity–dispersal relationship as special cases. Loreau *et al.*’s (2003a) model is closely related to ours, except that it also includes environmental fluctuations. However, these fluctuations have a small effect on the predicted diversity–dispersal relationship (Appendix S6). Loreau *et al.* (2003a) did not consider resource dispersal and they studied only a specific set of parameter values for which one generalist excludes the other species for large consumer dispersal (and without resource dispersal). This explains why they predicted a hump-shaped diversity–dispersal relationship. However, as we have stressed above, this prediction is contingent on a particular choice of parameter values. The same model can lead to other diversity–dispersal relationships for slightly different parameter values. For example, by decreasing niche overlap between species, species coexistence is facilitated and the diversity–dispersal relationship reaches higher diversity values for large consumer dispersal (Appendix S6). Mouquet & Loreau’s (2003) model is rather different from ours, because it is based on a lottery competition instead of the mechanistic resource competition described by ours. Nevertheless, it can be interpreted in our framework by noting that in their model the limit of large dispersal homogenises the metacommunity. This corresponds to the joint limit of large consumer dispersal and large resource dispersal in our model. As a result, our theory predicts a hump-shaped diversity–dispersal relationship, as reported by Mouquet & Loreau (2003). Interestingly, although both Loreau *et al.* (2003a) and Mouquet & Loreau (2003) predicted that the diversity–dispersal relationship drops to zero at large dispersal, they did so for different reasons. In Mouquet & Loreau (2003), large dispersal homogenises the metacommunity, so that no diversity can be maintained. In Loreau *et al.* (2003a), large (consumer) dispersal does not homogenise the metacommunity (the resource distribution is heterogeneous), but it increases the competitive advantage of a generalist species, which excludes all other species. Thus, our theory unifies previous results by considering the combined effects of consumer dispersal and resource dispersal.

It is worth noting, however, that models with a more implicit description of species competition do not necessarily predict hump-shaped diversity–dispersal relationships either. For example, the metacommunity model with local Lotka-Volterra competitive interactions (used, e.g., in Levin 1974; Amarasekare & Nisbet 2001),

$$\frac{\mathrm{d}N_{ik}}{\mathrm{d}t} = \frac{r_{ik}N_{ik}}{K_{ik}}\left(K_{ik} - \sum_j a_{ijk}N_{jk}\right) + \alpha(\langle N_i\rangle - N_{ik}), \tag{5}$$

also leads to a range of diversity–dispersal relationships depending on the choice of parameter values (intrinsic growth rates r_{ik}, carrying capacities K_{ik} and competition coefficients a_{ijk}). The predicted relationships are similar to those of our model without resource dispersal. In fact, there is a formal equivalence between, on the one hand, model (5) and, on the other hand, model (1) without resource dispersal and with fast resource dynamics. This equivalence is analogous to that between the non-spatial Lotka-Volterra competition model and the non-spatial consumer-resource model with fast resource dynamics (MacArthur 1972; Abrams *et al.* 2008). Hence, model (5) with large dispersal corresponds to model (1) with large consumer dispersal and small resource dispersal and not to model (1) with large consumer dispersal and large resource dispersal. In other words, model (5) implicitly assumes a heterogeneous resource distribution, even though consumer dispersal α is large. This illustrates the relevance of our theory for a larger class of metacommunity models and, more generally, the importance of taking into account spatial resource flows in metacommunity models.

Our results indicate that the experimental setup used to manipulate dispersal can change the diversity–dispersal relationship qualitatively [compare Fig. 4, panels (c) and (d)]. If consumer dispersal is varied without affecting resource dispersal (e.g. by sowing different amounts of seeds in plant metacommunities), then a range of diversity–dispersal relationships is possible. If a variation in consumer dispersal entails a simultaneous variation in resource dispersal (e.g. by transferring different volumes of water in aquatic metacommunities), then the diversity–dispersal relationship should be hump-shaped. On the whole, the hump-shaped relationship should not be considered as a hallmark of metacommunity structure. The meta-analysis of Cadotte (2006) was explicitly directed at detecting a hump-shaped pattern in experimental studies. It might be more insightful to allow for a wider range of possible relationships, thereby taking into account the experimental set-up used to manipulate dispersal. Cadotte (2006) obtained ambiguous results for the strong-dispersal part of the diversity–dispersal relationship, precisely where our model predictions deviate from previous metacommunity models.

Our study implies that one-dimensional diversity–dispersal relationships are not as strong an experimental test of metacommunity theory as previously thought. Two-dimensional relationships, in which consumer dispersal and resource dispersal are varied independently, would be more instructive about the underlying metacommunity processes. Such a relationship could be measured, e.g. in the Metatron, a large-scale experimental setup for multitrophic terrestrial metacommunities (Legrand *et al.* 2012). Strong tests of the predicted metacommunity patterns would result from considering a large number of combinations of consumer dispersal and resource dispersal, spanning the range from small to large values (Fig. 1). A preliminary two-dimensional relationship was measured by Limberger & Wickham (2011), studying the effects of prey and predator dispersal on prey diversity (rather than predator diversity as in this study). Several studies have investigated the effect of resource levels on metacommunity structure (Kneitel & Miller 2003; Cadotte *et al.* 2006; Matthiessen *et al.* 2010). Our model could also serve as a theoretical framework for these experiments (see Figs S3 and S4). Finally, we have described the effects of consumer and resource dispersal on the presence of specialist vs. generalist species. We found a simple pattern that to our knowledge has not been described previously (Kneitel & Chase 2004). This pattern can be studied experimentally, or could be useful to interpret observational data (Pandit *et al.* 2009).

A current challenge in metacommunity theory is to integrate trophic structure into spatial community models (Holt 2002; McCann *et al.* 2005; Amarasekare, 2008a, b; Pillai *et al.* 2011). Our spatial consumer-resource model, which may be viewed as a metacommunity model with two trophic levels, is a new step towards this goal. Our analysis of this model was based on an analytical study of limiting cases assuming very small or very large dispersal values, complemented with numerical simulations for intermediate dispersal values. By combining these tools, we have obtained a broad and detailed understanding of the model. We suggest that a similar approach will be useful to investigate metacommunity models with more intricate trophic structure.

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AUTHORSHIP

BH and ML designed the study; BH analysed the model; and BH and ML wrote the manuscript.

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