vol. 185, no. 1 the american naturalist january 2015

E-Article

A Graphical-Mechanistic Approach to Spatial Resource Competition

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Submitted March 18, 2014; Accepted August 1, 2014; Electronically published December 2, 2014

Online enhancement: appendixes.

abstract: Ecological communities are structured by processes operating at multiple spatial scales, which results in an often daunting complexity. Here we present a simple graphical theory to study the interaction of two fundamental community processes: resource competition at the local scale and dispersal at the regional scale. We consider a metacommunity model with two habitat patches in which consumer species compete for a spatially distributed resource. We introduce a graphical construction of the equilibrium metacommunity composition, analogous to traditional competition theory for two resources. As in the nonspatial case, the zero net growth isoclines (ZNGIs) play a central role in the analysis. We show that a consumer species' ZNGI depends on its dispersal characteristics, and this dependence leads to a unification of various dispersal-based coexistence mechanisms. We illustrate this unification using four specific mechanisms: species-specific dispersal rates, spatially asymmetric dispersal, resource-dependent dispersal, and competition between habitat specialists and generalists.

Keywords: dispersal, informed dispersal, metacommunity, resource competition, spatial heterogeneity, species coexistence, zero net growth isocline.

Introduction

Ecological communities are spatially extended systems in which processes at different scales interact (Ricklefs 1987; Levin 1992; Chave 2013). One of the theoretical efforts to capture this spatial complexity is the metacommunity framework (Leibold et al. 2004; Holyoak et al. 2005; Logue et al. 2011). In this framework, an ecological community is no longer viewed as an isolated, spatially uniform system but as a regional network of spatially interconnected local communities. A major challenge is to extend the theoretical body of community ecology—often obtained by neglecting spatial structure—to the metacommunity scale.

Resource competition is one of the most fundamental community processes (MacArthur 1972; Grover 1997). Competition theory for a single resource is elegantly summarized by the R^* rule. This rule states that the consumer species with the lowest equilibrium resource requirement excludes the other consumer species. Competition theory for two resources lacks such a simple rule, but it can be studied using a graphical analysis (Tilman 1980, 1982). In this analysis, the resource requirements of each consumer species are represented by a zero net growth isocline (ZNGI). The relative position of the ZNGIs determines the outcome of competition. The graphical theory of resource competition has a long history (MacArthur 1972; Leó 1975) with several important extensions (Tilman 1988; Holt et al. 1994; Leibold 1996) and interesting recent developments (Ballyk and Wolkowicz 2011; Ryabov and Blasius 2011).

Although competition for a spatially distributed resource has been extensively studied (Grover 1997; Amarasekare 2003), a theory of the same clarity as that of nonspatial resource competition has still to be developed. Here we contribute to this goal by proposing a graphical theory of spatial resource competition. Tilman (1982) already considered a spatially heterogeneous environment, but he assumed that consumers cannot move. Here we explicitly integrate the dispersal process into the consumer-resource dynamics. Ryabov and Blasius (2011) studied resource competition along a continuous resource gradient. Instead, we consider a metacommunity consisting of two discrete habitat patches, which allows us to considerably simplify the graphical analysis. This approach is very similar to the graphical analysis that Leibold and Tessier (1997) applied to a lake ecosystem of zooplankton consumers and phytoplankton resources. By distinguishing two water layers with distinct environmental conditions (temperature and illumination) affecting zooplankton ecology (growth and predation), they analyzed how this spatial structure determines zooplankton community composition. Here we

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Am. Nat. 2015. Vol. 185, pp. E1–E13. © 2014 by The University of Chicago. 0003-0147/2015/18501-55360$15.00. All rights reserved.
DOI: 10.1086/679066

generalize this approach and propose a general theoretical framework to analyze the effects and visualize the mechanisms of spatial resource competition. As in the nonspatial case, the analysis is based on the ZNGIs of the consumer species, which capture their spatial resource requirements and determine their chances to win spatial resource competition.

Although the theory of nonspatial resource competition can be viewed as predictive, its empirical support is surprisingly weak (Miller et al. 2005; but see Wilson et al. 2007). In fact, the main success of resource competition theory lies not in its direct predictions but rather in the conceptual frame of reference it has established. The impact of resource competition theory is clearly illustrated by the prominent position it occupies in most ecology textbooks. Similarly, we view the spatial variant of the theory first and foremost as a conceptual clarification of how the omnipresent community processes of resource competition and dispersal interact. To clearly exhibit the mechanisms involved, we simplify the model as much as possible. Subsequently, we discuss the effect of relaxing these simplifying assumptions as well as the connection with empirical systems and, in particular, with Leibold and Tessier's (1997) approach to zooplankton coexistence.

We illustrate the strength of this conceptual approach by unifying and generalizing previous fragmentary results on the effects of dispersal on resource competition. First, it has been reported that the outcome of (nonspatial) resource competition can be altered if consumer species have different dispersal rates (Abrams and Wilson 2004; Namba 2007). Second, Salomon et al. (2010) described conditions for spatially asymmetric dispersal to induce the coexistence of an inefficient consumer species with a more efficient one. Third, it is known that a species with the ability to change its dispersal rate on the basis of an environmental clue (such as the local density of conspecifics) can gain a competitive advantage (Armsworth and Roughgarden 2005; Amarasekare 2010). Fourth, Haegeman and Loreau (2014) showed that dispersal can affect the outcome of competition between habitat specialists and generalists. We show that from the perspective of our graphical theory, these various results can be explained by a single mechanism, namely, the dependence of a consumer species' ZNGI on its dispersal characteristics.

Spatial Consumer-Resource Model

We study the mechanisms of spatial resource competition using a simple metacommunity model (Loreau et al. 2003). We consider consumer species competing for a single limiting resource that is spatially distributed. Consumers have species-specific habitat preferences and can disperse through the community. Their competitive ability is determined by the interaction of local (resource consumption) and regional (dispersal) processes. For simplicity, we restrict our attention to a metacommunity consisting of two patches. This restriction will enable a two-dimensional graphical analysis, which is developed later.

First, let us consider consumer dynamics. We denote by N_{ik} the biomass of species i in patch k and by R_k the amount of resource in patch k. The local dynamics are governed by resource consumption, while the local patches are coupled through dispersal. The dynamical equations for consumer species i are

$$\frac{\mathrm{d}N_{i1}}{\mathrm{d}t} = e_{i1}c_{i1}R_1N_{i1} - m_{i1}N_{i1} + (\alpha_{i21}N_{i2} - \alpha_{i12}N_{i1}),$$

$$\frac{\mathrm{d}N_{i2}}{\mathrm{d}t} = e_{i2}c_{i2}R_2N_{i2} - m_{i2}N_{i2} + (\alpha_{i12}N_{i1} - \alpha_{i21}N_{i2}). \qquad (1)$$

In patch k, species i consumes the resource at rate c_{ik}, converts it to new biomass with efficiency e_{ik}, and loses biomass at rate m_{ik}. For simplicity, we assume that growth depends linearly on the local amount of resource (we discuss the extension to nonlinear resource dependence in app. D; apps. A–E available online). Consumer species i disperses from patch k to patch ℓ with rate $\alpha_{ik\ell}$. Consumption rates, conversion efficiencies, loss rates, and dispersal rates are assumed to be patch dependent, modeling the response of consumers to local environmental conditions, such as temperature or the presence of a predator. It is worth noting that these patch dependencies are expected to be correlated. For example, the presence of a predator in one of the patches can simultaneously affect a species' consumption rate, conversion efficiency, loss rate, and dispersal rate in that patch (Werner and Peacor 2003).

Second, let us consider the dynamics of the resource, which we assume to be abiotic (we discuss the case of a biotic resource in app. C). The resource in patch k is supplied at rate a_kA_k and lost at rate a_k, leading to the dynamical equations

$$\frac{\mathrm{d}R_1}{\mathrm{d}t} = a_1(A_1 - R_1) - \sum_i c_{i1}N_{i1}R_1,$$

$$\frac{\mathrm{d}R_2}{\mathrm{d}t} = a_2(A_2 - R_2) - \sum_i c_{i2}N_{i2}R_2. \qquad (2)$$

The resource dynamics are spatially heterogeneous through the patch dependence of the resource parameters a_k and A_k and of the consumption rates c_{ik}. Note that in the absence of consumers, the equilibrium amount of resource in patch k is equal to either A_k. We call the parameter A_k the resource supply to patch k.

In the special case where there is no dispersal, $\alpha_{i12} = \alpha_{i21} = 0$, and the dynamics of the two patches are decoupled. The equilibrium composition of a patch can then be determined using the R^* rule. The R^* value of species i in patch k is given by

$$R^*_{ik} = \frac{m_{ik}}{e_{ik}c_{ik}}. \tag{3}$$

If the R^* value of at least one species in patch k is smaller than the resource supply to patch k, then the species with the smallest R^* value in patch k excludes the other species at equilibrium. Otherwise, patch k is empty of consumers at equilibrium. In this article, we generalize this result to include the dispersal process.

Graphical Analysis

The model given by equations (1) and (2) combines consumer-resource dynamics at the local scale with consumer dispersal at the regional scale. Here we present a graphical construction of the equilibrium composition of the metacommunity. This construction is closely related to the graphical analysis of nonspatial resource competition theory with two resources (Tilman 1982; Grover 1997). The link with nonspatial resource competition theory is intuitive: a single resource distributed over two patches corresponds effectively to two distinct resources (Abrams 1988).

Analysis of Consumer Dynamics

As in the classical nonspatial theory of resource competition, the equilibrium of the model (eqq. [1], [2]) can be analyzed in two steps. In the first step, we consider the equilibrium conditions for the consumer dynamics (eq. [1]). Note that the equations for consumer species i do not depend on the biomass N_{j1} and N_{j2} of consumer species j. The dynamics for different consumer species are coupled only through the resource levels R_1 and R_2. In fact, we can decouple the consumer dynamics by assuming that the resource levels are fixed. That is, in this first step of the analysis, we consider the resource variables R_1 and R_2 as parameters. Although this assumption changes the consumer dynamics qualitatively (it removes the density dependence mediated by the resource), we can take into account their coupling by resource dynamics separately in the second step of the analysis.

For each consumer species i, we set $\mathrm{d}N_{i1}/\mathrm{d}t = 0$ and $\mathrm{d}N_{i2}/\mathrm{d}t = 0$. These equations are linear in the variables N_{i1} and N_{i2} and can be written in matrix form:

$$\begin{bmatrix} e_{i1}c_{i1}R_1 - m_{i1} - \alpha_{i12} & \alpha_{i21} \\ \alpha_{i12} & e_{i2}c_{i2}R_2 - m_{i2} - \alpha_{i21} \end{bmatrix} \begin{bmatrix} N_{i1} \\ N_{i2} \end{bmatrix} = 0. \tag{4}$$

They are trivially satisfied if $N_{i1} = N_{i2} = 0$. If this were the only solution, species i would be absent from the metacommunity at equilibrium. Other nontrivial solutions are possible only if the matrix in equation (4) is singular; that is,

$$\det\left(\begin{bmatrix} e_{i1}c_{i1}R_1 - m_{i1} - \alpha_{i12} & \alpha_{i21} \\ \alpha_{i12} & e_{i2}c_{i2}R_2 - m_{i2} - \alpha_{i21} \end{bmatrix}\right) = 0. \tag{5}$$

This equation imposes a relation between the resource levels at equilibrium R_1 and R_2. This relation has to be satisfied if species i is present in the metacommunity at equilibrium.

Graphically, equation (5) defines a curve in the plane (R_1, R_2), as illustrated in figure 1. This curve can be interpreted as follows. If the resource point is below the curve in equation (5)—that is, on the same side as the origin—the total biomass $N_{i1} + N_{i2}$ of species i decreases steadily. If the resource point is above the curve in equation (5), the biomass of species i increases steadily. Only if the resource is kept fixed at amounts located exactly on the curve does the biomass of species i remain constant. Therefore, the curve defined by equation (5) generalizes the ZNGI as used in the graphical analysis of nonspatial resource competition theory.

Interestingly, the ZNGIs of spatial resource competition theory depend on the dispersal of consumer species (fig. 1*A*). Without dispersal, the ZNGI is composed of a vertical part and a horizontal part (blue curve). On the vertical part, the amount of resource in patch 1 is equal to the species' R^* value in patch 1, so that the species can persist in patch 1. The amount of resource in patch 2 is smaller than the species R^* value in patch 2, so that the species biomass in patch 2 declines steadily. Hence, at equilibrium, the consumer biomass is concentrated on patch 1. On the horizontal part, the roles of patch 1 and patch 2 are inverted, and the consumer biomass is concentrated on patch 2. Clearly, if the resource is kept fixed at a point of the ZNGI, the consumer species can persist in at least one patch.

With dispersal, the consumer species cannot persist if the resource is kept fixed at a point on the blue curve (i.e., the ZNGI in the case without dispersal). To see this, assume that the resource is fixed at a point on the vertical part of that curve. Because of dispersal, the biomass is distributed over the two patches. The part of the biomass in patch 1 has zero net growth, but the part of the biomass in patch 2 declines, so that the total amount of biomass declines. Hence, the species cannot be maintained at equilibrium. For the species to be present at equilibrium, the decline in patch 2 has to be compensated by net growth in patch 1. That is, the resource should be fixed at a point in the

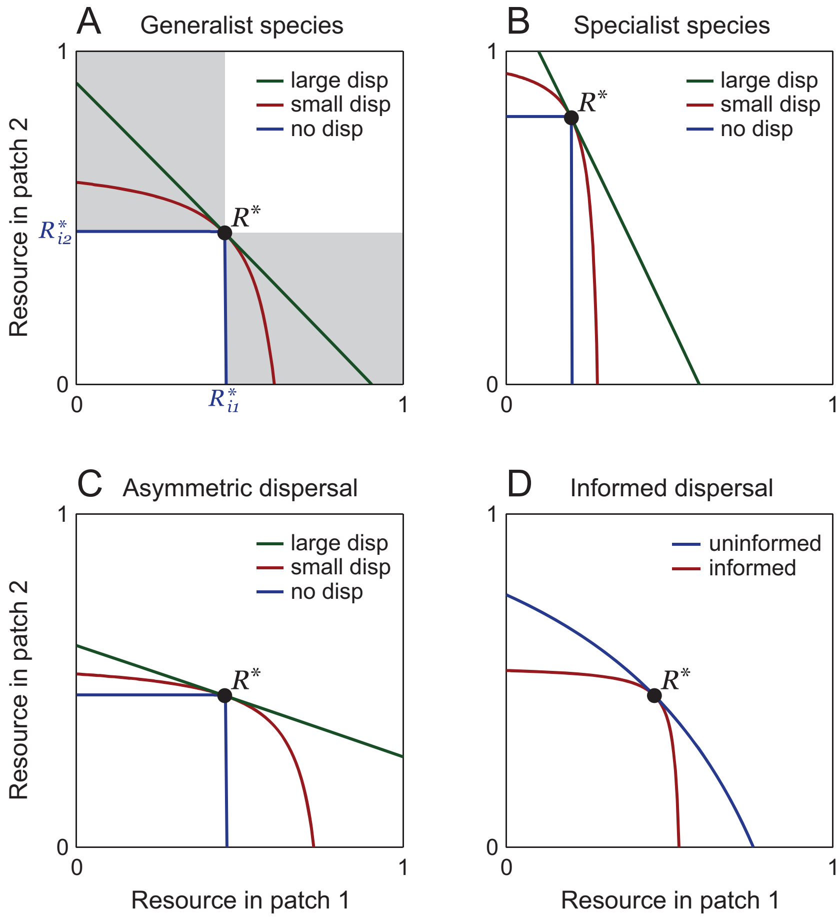


Figure 1: Zero net growth isoclines (ZNGIs). *A*, Effect of increasing dispersal (disp) rate for a generalist species. All ZNGIs pass through the species' R^* point with coordinates (R^*_{i1}, R^*_{i2}). The gray regions correspond to resource points with local decline in one patch and net growth in the other. *B*, Effect of increasing dispersal rate for a specialist species (specialization on patch 1). *C*, Effect of increasing dispersal rate when dispersal is asymmetric (dispersal is stronger from patch 1 to patch 2 than from patch 2 to patch 1). *D*, Effect of informed dispersal (negative resource dependence of the dispersal rate). Parameter values are given in appendix A, available online.

gray bottom right portion of figure 1*A*. Similarly, the gray top left portion of figure 1*A* corresponds to amounts of resource for which the species' biomass declines in patch 1 but grows in patch 2. As a result, the ZNGIs in the case with dispersal lie inside the gray regions, as illustrated by the red and green curves. The green curve corresponds to a larger dispersal rate than does the red curve. A larger dispersal leads to a larger shift of the biomass to the unfavorable patch, so that the local decline in the unfavorable patch has to be compensated more strongly by the net growth in the favorable patch. Hence, the ZNGIs move toward larger amounts of resource when increasing dispersal. Note that all ZNGIs of consumer species *i* have a common resource point, given by $R_1 = R^*_{i1}$ and $R_2 = R^*_{i2}$. For these amounts of resource, the species has zero net growth in both patches. Therefore, the species can persist in the two-patch metacommunity for any dispersal rate at this point. We call point (R^*_{i1}, R^*_{i2}) the R^* point of species *i*.

A similar reasoning as for the habitat generalist of figure 1*A* holds for a habitat specialist (fig. 1*B*). The species is specialized on patch 1: in patch 1, its consumption rate is larger and/or its loss rate is smaller than in patch 2. The ZNGIs for three dispersal values are shown in blue, red, and green as before. Without dispersal (blue curve), only a small amount of resource in patch 1 is required to maintain the species, whereas a much larger amount of resource is required in patch 2. Hence, the ZNGI is elongated along the R_2-axis. When increasing dispersal (red and green curves), the ZNGIs move toward larger amounts of resource, as for the generalist species. The ZNGIs share the R^* point of the specialist species and are elongated along

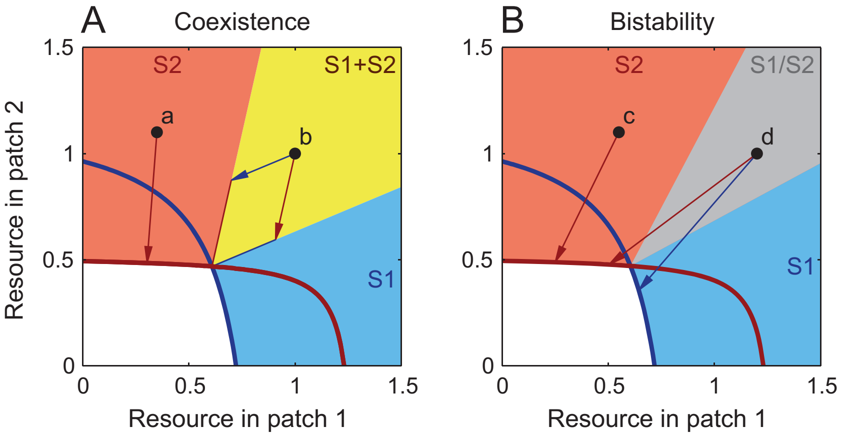


Figure 2: Resource supply diagrams. Species S1 (blue) and S2 (red) compete for a spatially distributed resource. Different outcomes are possible: no species can persist (white region); only species S1 can persist (blue region); only species S2 can persist (red region); species S1 and S2 coexist (yellow region); and either species S1 or species S2 persists, depending on initial conditions (gray region). *A*, Consumption vectors are drawn for resource supply points a and b. *B*, Same as *A* but with different consumption vectors. Consumption vectors are drawn for resource supply points c and d. Parameter values are given in appendix A, available online.

the R_2-axis. Similarly, the ZNGIs of a species specialized on patch 2 would be elongated along the R_1-axis.

Not only the magnitude of the dispersal rate but also other dispersal characteristics affect a species' ZNGI. As an example, we consider asymmetric dispersal, that is, a difference in dispersal rates α_{i12} (from patch 1 to patch 2) and α_{i21} (from patch 2 to patch 1). Figure 1*C* shows the ZNGIs of a species that disperses more strongly from patch 1 to patch 2 than from patch 2 to patch 1. When increasing dispersal, the ZNGI shifts more to larger amounts of resource in the bottom right portion (where decline in patch 2 is compensated by growth in patch 1) than in the top left portion (where decline in patch 1 is compensated by growth in patch 2). As a result, the species' ZNGI becomes elongated along the R_1-axis. Similarly, the ZNGI of a species that disperses more strongly from patch 2 to patch 1 than from patch 1 to patch 2 would be elongated along the R_2-axis when increasing dispersal. The effect of informed dispersal on the ZNGIs, illustrated in figure 1*D*, is discussed in "Informed Resource-Dependent Dispersal."

Once we have determined the ZNGI of each consumer species *i*, we can combine their ZNGIs in a way analogous to nonspatial resource competition theory. For a species to be present at equilibrium, the resource point (R_1, R_2) should lie on its ZNGI. For two species to be present at equilibrium, the resource point should lie at the intersection of their ZNGIs. Because three curves do not generically intersect at a single point, we find that at most two consumer species can coexist at equilibrium, globally and locally. Also, we have noted that the total biomass of a species steadily increases if the resource point (R_1, R_2) lies above its ZNGI. Hence, only a resource point (R_1, R_2) that lies on the ZNGI of at most two species and below the ZNGIs of all other species can lead to a stable equilibrium.

Analysis of Resource Dynamics

In the first step of the equilibrium analysis, we have characterized each consumer species by its ZNGI. In the second step, we now consider the equilibrium conditions for the resource dynamics (eq. [2]). The construction of the equilibrium community composition is similar to that of nonspatial resource competition theory. Here we give a sketch of the analysis, while we refer to appendix B for details.

The equilibrium conditions $\mathrm{d}R_1/\mathrm{d}t = 0$ and $\mathrm{d}R_2/\mathrm{d}t = 0$ can be schematically written as

$$\begin{aligned}&\text{equilibrium resource point} - \text{resource supply point}\\&= \sum_i \text{consumption vector of species } i \times N_i, \qquad (6)\end{aligned}$$

with $N_i = N_{i1} + N_{i2}$ the total biomass of species *i* (for an explicit expression, see eq. [B4]). Equation (6) expresses how at equilibrium resource consumption changes the amount of resource in the patches. Without consumers, the resource levels would be equal to the resource supplies A_1 and A_2. The presence of consumers reduces the resource to the equilibrium levels R_1 and R_2. This reduction (left-hand side of eq. [6]) can be written as a sum of consumption vectors over the consumer species present at equilibrium (right-hand side of eq. [6]).

The solution of equation (6) is illustrated in figure 2*A*. The ZNGIs indicate that species S1 (blue) prefers patch 1 and that species S2 (red) prefers patch 2. For resource supply point a, the resource is mainly supplied to patch

2 so that species S2 excludes species S1. Equation (6)—together with the condition that the equilibrium resource point (R_1, R_2) lies on the species' ZNGI—allows us to determine the three unknowns, N_2, R_1, and R_2 (for details, see eq. [B5]). For resource supply point b, the resource supply to the two patches is more balanced so that species S1 and S2 coexist at equilibrium (each species is present in both patches). The equilibrium resource point (R_1, R_2) is located at the intersection of the two species' ZNGIs. Equation (6) allows us to determine the species' biomasses N_1 and N_2 (for details, see eq. [B6]). As illustrated in the figure, the sum of the consumption vectors connects the resource supply point to the equilibrium resource point.

This analysis leads to a classification of the metacommunity equilibria as a function of the resource supply point (A_1, A_2). If the resource supply point lies below the ZNGI of each species (white region in fig. 2*A*), then no species can persist in the metacommunity. If the resource supply point lies in the blue or red region, then a single species dominates the metacommunity (the blue or red species, respectively). If the resource supply point lies in the yellow region, then the blue and red species coexist at equilibrium (each species is present in both patches). The boundary between the blue and yellow regions is a line the direction of which is given by the consumption vector of the blue species at the intersection of the ZNGIs. Similarly, the boundary between the red and yellow regions is determined by the consumption vector of the red species at the intersection of the ZNGIs. In summary, the resource supply diagram consists of several resource supply regions, each corresponding to a different metacommunity equilibrium.

As in nonspatial resource competition theory, the equilibrium community composition can exhibit priority effects, illustrated in figure 2*B*. For resource supply point c, species S2 excludes species S1 for any initial condition, as for resource supply point a. For resource supply point d, however, the outcome is different than for resource supply point b. There are two stable equilibria: one in which species S2 excludes species S1 (red consumption vector) and another in which species S1 excludes species S2 (blue consumption vector). Initial conditions determine to which equilibrium the metacommunity converges. If species S1 (species S2) is dominant in the initial condition, then competitive exclusion by species S1 (species S2) is likely. This bistability phenomenon occurs for any resource supply point in the gray region. These results are supported both by numerical stability analyses and by simulations of the dynamical system (eqq. [1], [2]).

A graphical invasibility analysis (app. B, fig. B1) suggests that the stability properties of the spatial system are analogous to those of the nonspatial system. Whether a resource supply region corresponds to stable coexistence (yellow region in fig. 2*A*) or bistability (gray region in fig. 2*B*) depends on the relative orientation of the species' consumption vectors and their ZNGIs. Specifically, if each species consumes proportionally more resource (determined by the consumption vectors) in the patch in which it is proportionally more competitive (determined by the ZNGIs), then the species coexist at equilibrium. This condition holds for resource supply point b, because species S1 consumes relatively (compared with species S2) more resource in patch 1 than in patch 2, while species S1 is relatively (compared with species S2) more competitive in patch 1 than in patch 2. In the opposite case, one species dominates the metacommunity at equilibrium, and the dominating species is determined by priority effects. This is the case for resource supply point d, because species S1 consumes relatively less resource in patch 1 than in patch 2, while species S1 is relatively more competitive in patch 1 than in patch 2.

The condition distinguishing stable coexistence and bistability compares two related quantities: resource consumption and competitive ability. If a consumer species has a large consumption rate in a patch (large c_{ik}), it is expected to be a good competitor in that patch (R^*_{ik} depends inversely on c_{ik}). Because the condition for bistability requires a negative correlation between resource consumption and competitive ability, the model (eqq. [1], [2]) suggests that bistability should be less common than stable coexistence. Note that the condition for bistability can be satisfied if species that have a large/small consumption rate in a patch also have a small/large conversion efficiency in that patch (because R^*_{ik} depends on the product $e_{ik}c_{ik}$). We implemented such a negative correlation between consumption rates c_{ik} and conversion efficiencies e_{ik} to choose parameter values in figure 2*B* (see app. A). However, although consumption rates and conversion efficiencies are often spatially heterogeneous (e.g., for patches at different temperatures), we do not expect negative correlations between them and the ensuing bistability to be common in real systems (see "Discussion").

Dispersal-Based Coexistence Mechanisms

We have shown how the consumer species' ZNGIs determine the equilibrium metacommunity composition. A species' ZNGI encodes its dispersal characteristics, and the relative position of the ZNGIs determines which species persist in the metacommunity. Here we use our graphical theory to study several dispersal-based coexistence mechanisms. Although these mechanisms have been described previously using different models, our analysis shows that they are conceptually closely related.

Species-Specific Dispersal

Species differences in dispersal rate together with spatial heterogeneity are considered as an important driver of metacommunity structure (Amarasekare 2008). For example, Abrams and Wilson (2004) showed that differences in species-specific dispersal rates allow an inefficient consumer species to coexist with a more efficient one. Here we show that their results can be readily obtained using our graphical framework.

The resource supply diagram of this coexistence mechanism is shown in figure 3. Without dispersal, the ZNGI of the more efficient consumer species S1 (blue) lies below the ZNGI of the inefficient consumer species S2 (red; fig. 3*A*). Hence, species S1 excludes species S2 for any resource supply point (except if the resource supplies are too small so that species S1 cannot persist). With dispersal, the species' ZNGIs shift to larger amounts of resource. The larger the dispersal rate, the larger this shift (fig. 1*A*). Therefore, if species S1 has a larger dispersal rate than does species S2, the ZNGI of species S1 can intersect the ZNGI of species S2, as illustrated in figure 3*B*. As a result, the resource supply diagram contains regions where both species coexist (yellow region) or where species S2 excludes species S1 (red region).

Clearly, the possibility of coexistence under this mechanism is due to the effect of dispersal on the species' competitive ability, depicted by their ZNGI. Note that this coexistence mechanism requires some form of spatial heterogeneity. In particular, if the species do not have any patch preference (i.e., consumption rate, conversion efficiency, loss rate, and dispersal rate are patch independent), as is the case in figure 3, then coexistence does not occur for equal resource supplies (the dashed line $A_1 = A_2$ lies within the region in which species S1 excludes species S2). The introduction of spatial heterogeneity in one of the species traits or in the resource supplies suffices to enable this coexistence mechanism to operate.

Spatially Asymmetric Dispersal

Much of the theory on the metacommunity-level consequences of dispersal assumes that the dispersal process is spatially homogeneous. However, in the real world, asymmetries in the spatial dispersal pattern are expected to be common because of, for example, altitude gradients, wind directions, or oceanic currents. In one of the few studies addressing this theoretical gap, Salomon et al. (2010) described a metacommunity in which this asymmetric dispersal allows an inefficient consumer species to coexist with a more efficient one. In a two-patch metacommunity, asymmetric dispersal means that a species' dispersal rate differs between dispersal directions (i.e., dispersal rate $\alpha_i 12$ from patch 1 to patch 2 differs from dispersal rate $\alpha_i 21$ from patch 2 to patch 1). Here we show that this mechanism can be easily understood using our graphical framework.

The resource supply diagram of this coexistence mechanism is shown in figure 4. Species S1 (blue) is a more efficient consumer than species S2 (red). For species-independent, symmetric dispersal, the ZNGI of species S1 lies below the ZNGI of species S2, so that species S1 excludes species S2 for any resource supply point (fig. 4*A*).

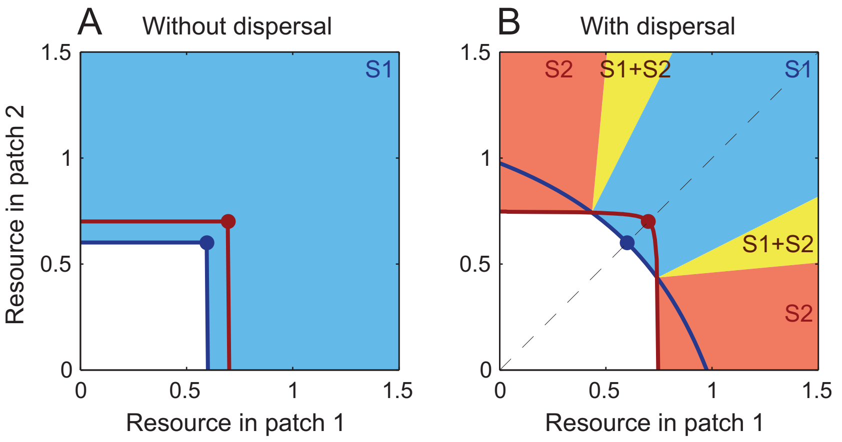


Figure 3: Differences in species-specific dispersal rates can induce species coexistence. Species S1 (blue zero net growth isocline [ZNGI], blue R^* point) is a more efficient consumer than species S2 (red ZNGI, red R^* point) in both patches. *A*, Without dispersal, species S1 excludes species S2 for all resource supplies (A_1, A_2) (blue region). *B*, Species S1 has a larger dispersal rate than does species S2. There are resource supplies (A_1, A_2) for which species S1 and S2 coexist (yellow regions) and for which species S2 excludes species S1 (red regions). The dashed line corresponds to equal resource supplies in the two patches. Parameter values are given in appendix A, available online.

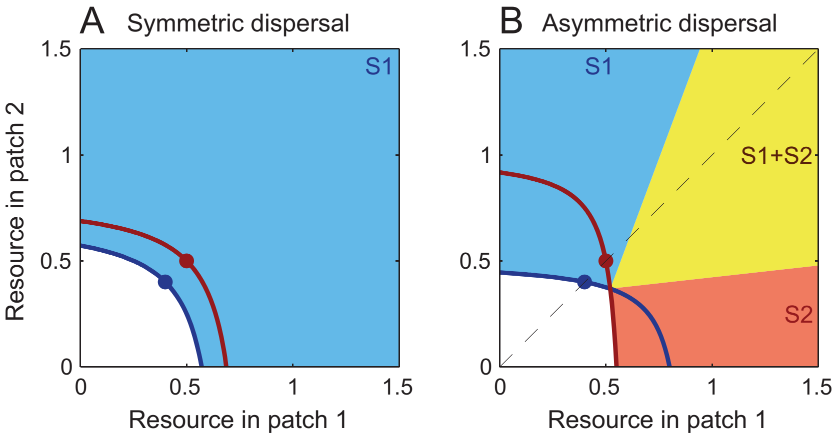


Figure 4: Asymmetric dispersal can induce species coexistence. Species S1 (blue zero net growth isocline [ZNGI], blue R^* point) is a more efficient consumer than species S2 (red ZNGI, red R^* point) in both patches. *A*, Dispersal is symmetric and species independent. Species S1 excludes species S2 for all resource supplies (A_1, A_2) (blue region). *B*, Dispersal is asymmetric with species S1 (species S2) preferentially dispersing to patch 2 (patch 1). There are resource supplies (A_1, A_2) for which species S1 and S2 coexist (yellow region) and for which species S2 excludes species S1 (red region). The dashed line corresponds to equal resource supplies in the two patches. Parameter values are given in appendix A, available online.

When dispersal is asymmetric, the species' ZNGIs become elongated along one of the resource axes (fig. 1*C*). We take $\alpha_{112} = \alpha_{221} > \alpha_{121} = \alpha_{212}$; that is, the dispersal asymmetry is symmetrical between the two species. Species S1 disperses preferentially from patch 1 to patch 2, so that its ZNGI becomes elongated along the R_1-axis. Symmetrically, species S2 disperses preferentially from patch 2 to patch 1, so that its ZNGI becomes elongated along the R_2-axis. These changes in the species' ZNGIs can make them intersect, as illustrated in figure 4*B*. As a result, the resource supply diagram contains a region where both species coexist (yellow region) and a region where species S2 excludes species S1 (red region).

As for species-specific dispersal, coexistence is due to the effect of dispersal characteristics on the species' ZNGI. However, in contrast to species-specific dispersal, coexistence is possible even for a spatially homogeneous system. In the example of figure 4*B*, although all species traits are patch independent, coexistence does occur for equal resource supplies (the dashed line $A_1 = A_2$ partially lies in the coexistence region). The species-specific dispersal asymmetry suffices to enable coexistence.

Informed Resource-Dependent Dispersal

In the previous examples, as in most spatial competition models, we assumed that dispersal rate is constant and independent of the environment. This widespread if unrealistic assumption (Clobert et al. 2009) can easily be relaxed within our graphical framework. To illustrate this, we consider a particular form of dispersal informed by the environment. For an individual deciding whether to disperse, the local resource level seems to be an obvious environmental clue to take into account. Hence, we assume that the dispersal rate depends on the amount of resource in the patch of the dispersing individual.

First, we extend the model (eqq. [1], [2]) to include resource-dependent dispersal rates. We assume that the dispersal rate α_{i12} from patch 1 to patch 2 depends linearly on the local amount of resource R_1 in patch 1 and that, similarly, the dispersal rate α_{i21} from patch 2 to patch 1 depends linearly on the local amount of resource R_2 in patch 2:

$$\begin{aligned} \alpha_{i12}(R_1) &= d_1 + d_2(R_1 - R_{i1}^*), \\ \alpha_{i21}(R_2) &= d_1 + d_2(R_2 - R_{i2}^*). \end{aligned} \tag{7}$$

Information about the local resource level yields a competitive advantage if a small local resource level induces a large emigration flow; that is, if $d_2 > 0$. Note that we use the species' R^* value as a point of reference, which is useful to compare species without and with resource-dependent dispersal. When varying resource dependence, the dispersal rate is constant at the R^* point (recall that the R^* point occurs on the ZNGI for any dispersal rate).

Figure 1*D* shows the effect of resource-dependent dispersal on the ZNGI. We consider a species with a constant dispersal rate (blue curve) and add negative resource dependence (red curves). The ZNGI shifts to smaller amounts of resource, which can be understood as follows. Consider the bottom right portion of the ZNGI, in which the species' net growth in patch 1 (because $R_1 > R_{i1}^*$) and local decline in patch 2 (because $R_2 < R^*_{i2}$) balance each other. Resource dependence decreases (increases) the dispersal rate from patch 1 to patch 2 (from patch 2 to patch 1), so that the biomass distribution is biased toward patch 1. Hence, smaller amounts of resource are required to compensate the decline in patch 2. A similar argument holds for the top left portion of the ZNGI. The graphical analysis quantifies the competitive advantage conferred by resource-dependent dispersal.

Negative resource dependence can make an inefficient consumer species coexist with a more efficient one. This can be clearly illustrated using the resource supply diagram of figure 5. Species S1 (blue) is a more efficient consumer than species S2 (red). For resource-independent dispersal, the ZNGI of species S1 lies below the ZNGI of species S2, so that species S1 excludes species S2 for any resource supply point (fig. 5*A*). When we introduce negative resource dependence in the dispersal of species S2, its ZNGI shifts to smaller amounts of resource, so that the ZNGIs of species S1 and S2 can intersect (fig. 5*B*). As a result, the resource supply diagram contains a region where both species coexist (yellow region) and a region where species S2 excludes species S1 (red region). As for the previous coexistence mechanisms, the possibility of coexistence originates from the change in the species' ZNGI induced by dispersal.

Coexistence of Specialists and Generalists

In a previous article, we studied the effect of dispersal on the coexistence of habitat specialists and generalists (Haegeman and Loreau 2014). Here we show that our findings can be clearly reformulated within our graphical framework.

In the model (eqq. [1], [2]), the habitat preferences of a species are encoded in its consumption rates, conversion efficiencies, and loss rates, and its competitive ability in the patches is quantified by its R^* values (eq. [3]). If the R^* values are comparable, the species is a generalist. If not, the species is specialized on the patch for which its R^* value is smallest. We assume the standard trade-off between generalists and specialists: in the patch on which it is specialized, a specialist is a better competitor than a generalist, but it is a worse competitor in the other patch.

We have discussed the ZNGIs of generalists and specialists in figure 1*A* and 1*B*. Whereas the ZNGI of a generalist species has a certain degree of symmetry between the resource axes, the ZNGI of a specialist species is elongated along one of the resource axes. The ZNGI of a species specialized on patch 1 (patch 2) is elongated along the R_2-axis (R_1-axis).

Resource competition between specialists and generalists can be analyzed using the resource supply diagrams of figure 6. We consider three consumer species: species S1 is specialized on patch 1 (blue), species S2 is specialized on patch 2 (red), and species G is a generalist (green). Without dispersal, specialist species S1 and S2 dominate their preferred patch and exclude the generalist species in both patches (fig. 6*A*). The specialists coexist on the metacommunity scale, but this coexistence is not mediated by dispersal. When increasing dispersal, the ZNGIs of the three species move to larger amounts of resource, but they

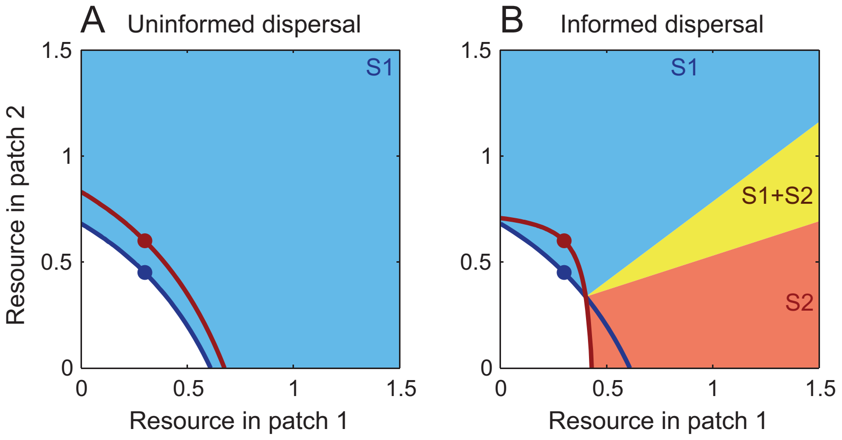


Figure 5: Informed dispersal can induce species coexistence. Species S1 (blue zero net growth isocline [ZNGI], blue R^* point) is a more efficient consumer than species S2 (red ZNGI, red R^* point) in both patches. *A*, Dispersal is resource independent. Species S1 excludes species S2 for all resource supplies (A_1, A_2) (blue region). B, Dispersal of species S2 has negative resource dependence. There are resource supplies (A_1, A_2) for which species S1 and S2 coexist (yellow region) and for which species S2 excludes species S1 (red region). Parameter values are given in appendix A, available online.

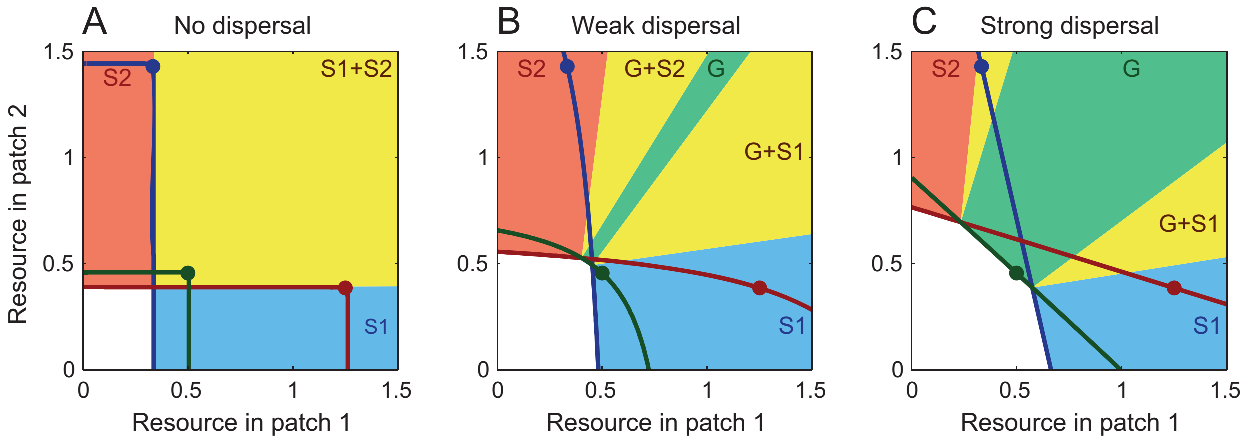


Figure 6: Dispersal can induce the coexistence of specialist and generalist species. Species S1 is a specialist for patch 1 (blue zero net growth isocline [ZNGI], blue R^* point). Species S2 is a specialist for patch 2 (red ZNGI, red R^* point). Species G is a generalist (green ZNGI, green R^* point). The dispersal rate (identical for all species) varies between panels. The colored regions indicate resource supply points for which different species persist: blue, species S1; red, species S2; green, species G; yellow, coexistence of two species. Parameter values are given in appendix A, available online.

do so in different ways (fig. 6*B*). This difference can be understood by considering the R^* point of the three species (recall that a species' R^* point occurs on its ZNGI for any dispersal rate). For the specialists, the R^* point lies away from the center of the diagram along a resource axis; for the generalist, the R^* point lies in the center of the diagram. This entails that in the center of the diagram, the specialists' ZNGIs move faster to larger amounts of resource than the generalist's ZNGI when increasing dispersal (the generalist's ZNGI is pinned at its R^* point; see also fig. 1*A*, 1*B*). Hence, the generalist's ZNGI can intersect the specialists' ZNGIs at smaller amounts of resource than at the intersection of the specialists' ZNGIs (fig. 6*C*). As a result, the resource supply diagram contains a region where the generalist excludes the specialists (green region) and two regions where the generalist coexists with one of the specialists (yellow regions). Note that these three regions correspond to resource supplies that are not too different ($A_1 \approx A_2$). Such resource supply points are especially favorable for the generalist.

Discussion

We have introduced a graphical method to analyze the outcome of spatial resource competition. Our approach, which extends the traditional theory of nonspatial resource competition, relies on the characterization of the resource requirements of the consumer species. We have represented these requirements as ZNGIs in the resource plane (which represents the amount of resource in the two patches). The relative position of the ZNGIs determines which consumer species persist if the spatial resource distribution is given. In turn, the spatial resource distribution is determined by the resource dynamics and, in particular, by the consumption characteristics of the consumer species. We have shown how the interaction of resource requirements and consumption characteristics can be represented in a resource supply diagram. In particular, the resource supply point determines which species coexist or exclude their competitors at equilibrium.

A key ingredient of our graphical analysis is the dependence of a consumer species' ZNGI on its dispersal characteristics. Although this dependence has not been considered formally so far, it should not come as a surprise. A single resource distributed over two patches is perceived by the consumer species as two distinct resources (Abrams 1988). Dispersal determines the amount of time that the consumers spend in each of the patches and, hence, the amount of time that each of the two effective resources is available for consumption. Therefore, dispersal affects the spatial resource requirements (i.e., the ZNGI) of the consumer species. We have shown that the dispersal dependence of the ZNGIs is not limited to the rate of dispersal but also includes dispersal characteristics such as spatial asymmetry and informed dispersal (e.g., resource dependence). By studying these dependencies, our approach has allowed us to unify a number of previously disconnected coexistence mechanisms into a single, coherent framework. It has also allowed us to extend existing theory and analyze the community-level consequences of informed dispersal (in particular, resource dependence).

There are numerous parallels between our graphical theory of spatial resource competition and the classical nonspatial resource competition theory. Note that because we have assumed that the same resource is present in both patches, the two effective resources correspond to substitutable resources in the nonspatial case. But our theory could be easily extended to patches containing different resources, which could be complementary. Also, as in the nonspatial case, the difference between stable coexistence and bistability lies in the relative position of ZNGIs and consumption vectors (compare fig. 2*A* and 2*B*). However, in the spatial case with the same resource in both patches, resource consumption is strongly influenced by the amount of time that consumers spend in each patch. A consumer species that spends more time in a specific patch is expected to consume more of the local resource and to be more limited by that resource. Although stable coexistence could be prevented by conversion efficiencies with strong species and/or patch dependencies, this scenario requires very special conditions and seems unlikely in real systems. Hence, coexistence due to habitat partitioning might be intrinsically more stable than coexistence due to within-habitat resource partitioning. It would be interesting to test this conclusion with empirical data.

Although the objective of our work was to provide a conceptual and mathematical framework to study spatial resource competition, our theory also suggests a number of possible empirical tests. We have deliberately kept the model as simple as possible (e.g., two patches, an abiotic resource, linear functional responses), which precludes the direct application of our model to real-world systems. In certain specific cases, however, simple extensions might suffice to overcome this obstacle. A nice illustration can be found in the work of Leibold and Tessier (1997), who analyzed zooplankton coexistence in a lake ecosystem using an approach very similar to ours (for a detailed discussion, see app. E). The lake ecosystem has a well-defined two-patch spatial structure, because plankton experiences very different ecological conditions in the warm, upper layer and in the cold, deep layer. Zooplankton organisms, when migrating between the two layers, modify their competitive ability. Leibold and Tessier's (1997) graphical model differs from ours because migration decreases the effective loss rate in one of the layers (for an explanation, see app. E). Also, their model was used to determine the optimal migration strategy a species adopts rather than taking the migration process for granted, as we did. Leibold and Tessier (1997) derived several predictions from their model, which they compared with observational data.

Although our simple model might not describe many natural systems as closely as that studied by Leibold and Tessier (1997), it should be possible to set up experimental metacommunities that implement assumptions very similar to those in our model. Aquatic microcosm metacommunities using unicellular organisms, in which resource supply and dispersal can be manipulated systematically (Kneitel and Miller 2003; Cadotte et al. 2006; Matthiessen et al. 2010), seem particularly suitable for testing our theory. Since resource supply and dispersal are at the core of the resource supply diagrams used in our graphical theory, it should be possible to build these diagrams for the experiments and to directly compare the experimental results with the theoretical predictions. If the dispersal intensity can be increased over a sufficiently large range, it would be interesting to create a series of resource supply diagrams, as in figure 6. If, in addition, it is possible to characterize individual species' competitive ability (i.e., to measure their ZNGI in single-species experiments), much finer theoretical predictions can be tested, because the ZNGIs determine the outcome of spatial resource competition to a large extent.

Comparison with empirical data, however, raises the question of the robustness of our theoretical results. Although this question goes beyond the scope of this article, we report a preliminary study of the case of a biotic resource (app. C) and of a model with nonlinear functional responses (app. D). These results indicate that our graphical analysis can be generalized up to a certain point but that the model can then also exhibit more complex behavior that cannot be analyzed with our approach. When relaxing the assumption of a two-patch metacommunity, a graphical analysis is no longer practical. However, the two-dimensional case provides a number of useful intuitions for larger metacommunities with $P > 2$ patches. In this case, the resource requirements of a consumer species (its generalized ZNGI) are described by a surface (of dimension $P - 1$) in a P-dimensional resource space. A species excludes the other species at a fixed resource distribution if the resource point lies on the species' ZNGI surface and below the ZNGI surface of the other species. In the case of a dynamically supplied resource, the P-dimensional resource space can be partitioned into resource supply regions to determine the metacommunity composition at equilibrium. These regions, determined by the species' consumption vectors, each correspond to a set of one up to P coexisting species. Similar remarks hold for multiple resources. In particular, if species compete for R resources in a metacommunity with P patches, the dimension of the resource space and the maximal number of coexisting species increases to PR. Moreover, apparent competition through a common predator can be dealt with in the same way as exploitation competition for a common resource. To do so, we have to augment the resource space with axes corresponding to the predator abundance in the various patches (Tilman 1982; Leibold 1996; Chesson and Kuang 2008).

Clearly, these higher-dimensional extensions point to the limitations of our graphical theory. Other limitations occur already in the simple two-patch metacommunity. A consumer species' ZNGI can be defined because the consumer dynamics (eq. [1]) can be analyzed separately from the resource dynamics (eq. [2]). For this to be possible, the right-hand side of the consumer dynamics (eq. [1]) should depend linearly on consumer biomass. Nonlinear dependencies appear if biomass loss or dispersal are density dependent, that is, if loss rate or dispersal rate depend on the biomass of conspecifics and/or heterospecifics. This implies that the graphical analysis can deal with only particular forms of informed dispersal. We have applied the graphical analysis to resource-dependent dispersal, but other forms of density-dependent dispersal should be investigated with other techniques.

Our analysis reveals that dispersal has a purely detrimental effect on species' competitive ability in our model. Once a consumer species becomes established in the patch in which it thrives best, dispersal moves part of its biomass to patches with less favorable growth conditions. This detrimental effect of dispersal results in the ZNGIs moving toward larger amounts of resource. Additional costs of dispersal can occur if there is mortality during the dispersal process. Additional gains can also occur if those individuals that disperse would die otherwise. If additional costs or gains of dispersal are introduced in the model, a consumer species' ZNGIs no longer pass through its R^* point (determined by the case without dispersal). Instead, the ZNGIs can have a more complex, nonmonotonic dependence on dispersal. These more complex cases, however, can be readily studied using our graphical analysis.

A more fundamental limitation of our approach (as of other graphical approaches) is the equilibrium assumption. Transient dynamics may be relevant, especially for the study of dispersal effects. A large dispersal rate allows consumer species to quickly leave/reach patches with deteriorating/improving growth conditions. Although this beneficial effect of dispersal is present in the model, its effects cannot be studied using our graphical framework. Building a systematic theory of the beneficial and detrimental effects of dispersal on spatial resource competition, including nonequilibrium behavior, is a challenge for further work.

Acknowledgments

We thank T. Day, C. de Mazancourt, M. Leibold, and two anonymous reviewers for helpful suggestions. This work was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41).

Literature Cited

Abrams, P. A. 1988. How should resources be counted? Theoretical Population Biology 33:226–242.

Abrams, P. A., and W. G. Wilson. 2004. Coexistence of competitors in metacommunities due to spatial variation in resource growth rates; does R^* predict the outcome of competition? Ecology Letters 7:929–940.

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

———. 2008. Spatial dynamics of foodwebs. Annual Review of Ecology, Evolution, and Systematics 39:479–500.

———. 2010. Effect of non-random dispersal strategies on spatial coexistence mechanisms. Journal of Animal Ecology 79:282–293.

Armsworth, P. R., and J. E. Roughgarden. 2005. The impact of directed versus random movement on population dynamics and biodiversity patterns. American Naturalist 165:449–465.

Ballyk, M. M., and G. S. Wolkowicz. 2011. Classical and resource-based competition: a unifying graphical approach. Journal of Mathematical Biology 62:81–109.

Cadotte, M. W., A. M. Fortner, and T. Fukami. 2006. The effects of resource enrichment, dispersal, and predation on local and metacommunity structure. Oecologia (Berlin) 149:150–157.

Chave, J. 2013. The problem of pattern and scale in ecology: what have we learned in 20 years? Ecology Letters 16:4–16.

Chesson, P., and J. J. Kuang. 2008. The interaction between predation and competition. Nature 456:235–238.

Clobert, J., L. Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197–209.

Grover, J. 1997. Resource competition. Population and Community Biology Series. Vol. 19. Chapman & Hall, London.

Haegeman, B., and M. Loreau. 2014. General relationships between consumer dispersal, resource dispersal and metacommunity diversity. Ecology Letters 17:175–184.

Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. American Naturalist 144:741–771.

Holyoak, M., M. A. Leibold, and R. D. Holt. 2005. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago.

Kneitel, J. M., and T. E. Miller. 2003. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. American Naturalist 162:165–171.

Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. American Naturalist 147:784–812.

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

Leibold, M. A., and A. J. Tessier. 1997. Habitat partitioning by zooplankton and the structure of lake ecosystems. Pages 3–30 *in* B. Streit, T. Stadler, and C. Lively, eds. Evolutionary ecology of freshwater animals. Birkhäuser, Boston.

León, J. A., and D. B. Tumpson. 1975. Competition between two species for two complementary or substitutable resources. Journal of Theoretical Biology 50:185–201.

Levin, S. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

Logue, J. B., N. Mouquet, H. Peter, and H. Hillebrand. 2011. Empirical approaches to metacommunities: a review and comparison with theory. Trends in Ecology and Evolution 26:482–491.

Loreau, M., N. Mouquet, and A. Gonzalez. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. Proceedings of the National Academy of Sciences of the USA 100:12765–12770.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. Princeton University Press, Princeton, NJ.

Matthiessen, B., E. Mielke, and U. Sommer. 2010. Dispersal decreases diversity in heterogeneous metacommunities by enhancing regional competition. Ecology 91:2022–2033.

Miller, T. E., J. H. Burns, P. Munguia, E. L. Walters, J. M. Kneitel, P. M. Richards, N. Mouquet, and H. L. Buckley. 2005. A critical review of twenty years' use of the resource-ratio theory. American Naturalist 165:439–448.

Namba, T. 2007. Dispersal-mediated coexistence of indirect competitors in source-sink metacommunities. Japan Journal of Industrial and Applied Mathematics 24:39–55.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. Science 235:167–171.

Ryabov, A. B., and B. Blasius. 2011. A graphical theory of competition on spatial resource gradients. Ecology Letters 14:220–228.

Salomon, Y., S. R. Connolly, and L. Bode. 2010. Effects of asymmetric dispersal on the coexistence of competing species. Ecology Letters 13:432–441.

Tilman, D. 1980. Resources: a graphical-mechanistic approach to competition and predation. American Naturalist 116:362–393.

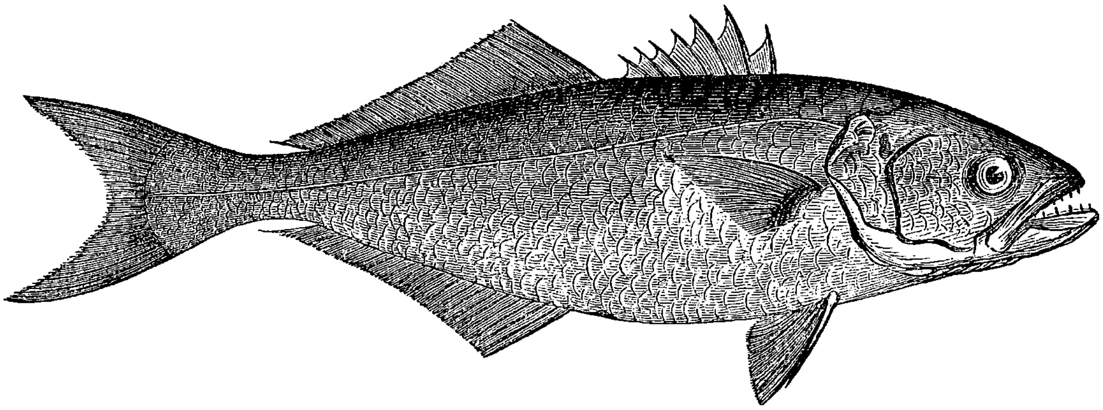
———. 1982. Resource competition and community structure. Monographs in Population Biology. Vol. 17. Princeton University Press, Princeton, NJ.

———. 1988. Plant strategies and the dynamics and structure of plant communities. Monographs in Population Biology. Vol. 26. Princeton University Press, Princeton, NJ.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100.

Wilson, J. B., E. Spijkerman, and J. Huisman. 2007. Is there really insufficient support for Tilman's R^* concept? a comment on Miller et al. American Naturalist 169:700–706.

Associate Editor: Mathew A. Leibold
Editor: Troy Day



"The Bluefish (*Temnodon saltator*) ... , which inhabits our waters from the last of June till September, has had very marked periodic variations in numbers. This fish, as history informs us, was captured and esteemed as an article of food by the earlier settlers of this state. Previous to the year 1763 bluefish were very plenty on the southern coast of Cape Cod, but about this year they all disappeared, and none were taken till sixty or seventy years after." From "The Habits and Migrations of Some of the Marine Fishes of Massachusetts" by James H. Blake (*The American Naturalist*, 1870, 4:513–521).