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Consequences of varying regional heterogeneity in source–sink metacommunities

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Although the influence of dispersal on coexistence mechanisms in metacommunities has received great emphasis, few studies have addressed how such influence is affected varying regional heterogeneity. We present a mechanistic model of resource competition in a metacommunity based on classical models of plant competition for limiting resources. We defined regional heterogeneity as the differences in resource supply rates (or resource availabilities) across local communities. As suggested by previous work, the highest diversify occurred at intermediate levels of dispersal among local communities. However our model shows how the effects of dispersal depend on the amount of heterogeneity among local communities and vice versa. Both regional and local species richness were the highest when heterogeneity was intermediate. We suggest that empirical studies that found no evidence for source–sink or mass effects at the community level may have examined communities with limited ranges of dispersal and regional heterogeneity. This model of species coexistence contributes to a broader understanding of patterns in real communities.

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Metacommunity ecology has recently developed a simple framework for incorporating spatial complexity into our understanding of natural communities (Leibold et al 2004, Holyoak et al. 2005). A metacommunity consists of a suite of local communities connected by dispersal of individuals across a larger region (Wilson 1992, Holt 1993). This perspective allows different mechanisms of species coexistence to be partitioned and understood at appropriate spatial scales. For example, if similar homogeneous habitats are spread across a region, species coexistence can result from appropriate trade offs between colonizing and competitive abilities (reviewed by Kneitel Chase 2004). In contrast, if an array of heterogeneous habitats is spread across a region, then variation in habitat-use efficiency among species may allow regional coexistence, and dispersal may promote local coexistence. This pattern is described as a mass effect (Shmida and Ellner 1984) or source–sink dynamics (Levin 1974, Holt 1993, Pulliam 2000, Mouquet and Loreau 2002).

Source–sink metacommunity models (also called “mass effect” models Leibold et al. 2004) link local and

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regional mechanisms of species coexistence and add a regional perspective to niche theory (Mouquet and Loreau 2003). High local species diversity is thought to be correlated with some level of regional heterogeneity, intermediate values of dispersal between communities, and a complementary distribution of competitive abilities at the scale of the region (spatial storage effect sensu Chesson 2000a or regional similarity sensu Mouquet and Loreau 2002). Aside from the original work by Shmida and Ellner (1984) on annual plant communities, few experiments have tested the source–sink mechanism for coexistence in natural systems, and empirical evidence in natural systems is still scant (Amarasekare 2003, Leibold and Miller 2004). Kunin (1998) found weak evidence of a mass effect between two neighbouring plant communities differing strongly in their local conditions. Cottenie et al. (2003), working in a series of interconnected ponds, found strong habitat heterogeneity among ponds but little evidence of mass effects despite significant rates of dispersal.

This lack of substantive evidence of source–sink dynamics might be the result of ecologists' focusing primarily on dispersal rather than on heterogeneity among local areas. Here, we argue that the condition of coexistence in source–sink metacommunities depends strongly on the level of regional heterogeneity. Following Kunin (1998), we propose that the highest species richness will be found at intermediate levels of heterogeneity in source–sink metacommunities. Heterogeneity has been defined differently in different contexts (Levin 1992). In metacommunities, regional heterogeneity can be expressed in terms of differences across local communities in the number of limiting factors. For example, Mouquet and Loreau (2003) have shown that increasing the number of communities differing in their local conditions potentially increases both local and regional species richness. Here we address another form of heterogeneity that is due to variation of environmental conditions among localities within the metacommunity. Because we focus on exploitative competition, we define regional heterogeneity as the differences among local communities in resource supply (Chase and Leibold 2003, Shurin et al. 2004).

To investigate the effects of dispersal and regional heterogeneity among local communities, we present a mechanistic model of resource competition in a metacommunity. The study reported here adds a regional perspective to the results of Tilman (1982) on environmental microheterogeneity and local species coexistence that is complementary to that previously proposed by Leibold and Chase (Leibold 1998, Chase and Leibold 2003).

A mechanistic model of competition in a metacommunity

To describe local interactions, we used a classical model of resource competition in which species interact through the consumption of two shared, essential resources (MacArthur 1972, Leon and Tumpson 1975, Tilman 1982, Chase and Leibold 2003). The original model developed by Leon and Tumpson (1975) reads:

$$\frac{dN_i}{dt} = N_i(\min[c_{i1}e_{i1}R_1, c_{i2}e_{i2}R_2] - d_i)$$

$$\frac{dR_1}{dt} = l_1(S_1 - R_1) - \sum_i \frac{N_i}{e_{i1}} \min[c_{i1}e_{i1}R_1, c_{i2}e_{i2}R_2] \qquad (1)$$

$$\frac{dR_2}{dt} = l_2(S_2 - R_2) - \sum_i \frac{N_i}{e_{i2}} \min[c_{i2}e_{i2}R_2, c_{i1}e_{i1}R_1]$$

where N_i is the abundance of species i, R_j is the quantity of resource j, c_{ij} is rate of consumption of resource j by species i, e_{ij} is conversion efficiency of resource j by species i (q of Leon and Tumpson 1975), d_i is the death rate of species i, S_j is the supply rate of the resource j, and l_jR_j is the rate of resource loss not due to consumption.

For each species, the break-even level of nutrient for which growth balances mortality is represented by a zero-net-growth isocline (ZNGI) on the phase plane of the two resources available in the environment (MacArthur 1972, Tilman 1982, reviewed by Chase and Leibold 2003). This model predicts that coexistence of the two species requires a number of conditions. First, the two ZNGI must cross one another (i.e., a trade off must exist between the sensitivity of each species to one resource and its sensitivity to the other). Second, the ratio of resources supplied must lie between the ratios consumed by the two species. Third, each species must consume more of the resource that limits its growth than of the non-limiting resource. A detailed analysis of these conditions is available in Leon and Tumpson (1975). Tilman (1982) used this framework to examine the effects of microscale heterogeneity on species coexistence. He considered a pool of species competing for two limiting resources, whose ZNGI cross one another and consumption ratios are such that multiple pairs of species can potentially coexist. Which pair of species actually coexist depends on the ratio of resources supplied to the system (Fig. 1). In such a context, Tilman defines micro-heterogeneity as when in a locality, the supply of resources to the system can be considered as coming from different sources ("microsites"). If microsites provide resources with different ratios, at a fine scale several pairs of species can simultaneously coexist (Fig. 36 in Tilman 1982) leading to potentially high species richness at the scale of the locality. These results have been interpreted at the regional scale by Leibold and Chase (Leibold 1998, Chase and Leibold 2003), who proposed that regional heterogeneity combined with trade offs in habitat-use efficiency promotes regional coexistence and that dispersal promotes species segregation (i.e. species sorting) at the regional scale.

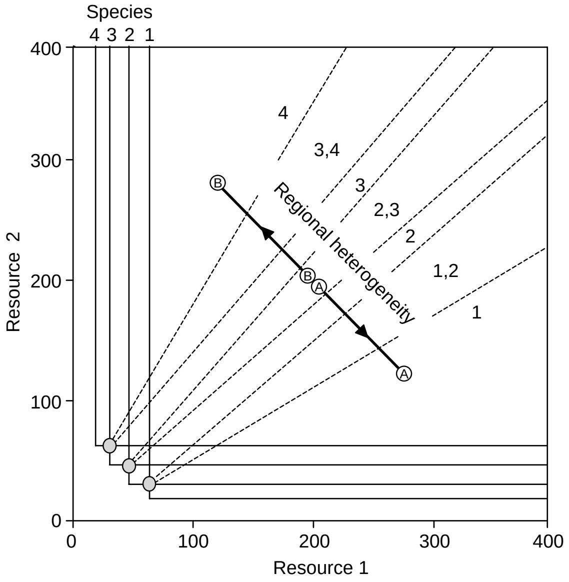

Fig. 1. Graphical analysis of competition model with four species (Eq. 1). The coordinates represent the quantities of two limiting resources available to the species. We have represented each species' zero-net-growth isocline and identify species by number. Any equilibrium point on the plane lies on an isocline. The large gray circles are two-species equilibria. The dashed lines define the area of supply points (S_1,S_2) which lead to the different equilibria. A supply point represents the level of inorganic nutrients in a system without plant (that is, the equilibrium values for R_1 and R_2 obtained by setting N_i to zero and the differential Eq. 1 to zero). The bold line shows how we generated the gradient of regional heterogeneity when we connected two communities (A and B) characterized by different resource supply points (chosen along that line). Parameters are $c_{11}=0.026$, $c_{12}=0.05$, $c_2=0.03$, $c_{22}=0.04$, $c_3=0.04$, $c_{32}=0.03$, $c_{41}=0.05$, $c_{42}=0.026$, $e_{11}=0.03$, $e_{12}=0.05$, $e_{21}=0.035$, $e_{22}=0.04$, $e_{31}=0.04$, $e_{32}=0.035$, $e_{41}=0.05$, $e_{42}=0.03$, $l_1=1$, $l_2=1$ and $d_i=0.05$ $\forall i$.

More recently, Shurin et al. (2004) have used a similar model to show how variation in resource supply ratios can generate alternative stable equilibria locally allowing high regional species richness.

To address the consequence of varying regional heterogeneity on coexistence, we applied this model (Eq. 1) to different local communities within a larger region (metacommunity) while incorporating the possibility of source–sink dynamics by considering explicit dispersal between the local communities. Building on Eq. 1 the metacommunity model reads:

$$\frac{dN_{iA}}{dt} = N_{iA}(\min[c_{i1}e_{i1}R_{1A}, c_{i2}e_{i2}R_{2A}] - d_i) + a(N_{iB} - N_{iA})$$

$$\frac{dN_{iB}}{dt} = N_{iB}(\min[c_{i1}e_{i1}R_{1B}, c_{i2}e_{i2}R_{2B}] - d_i) + a(N_{iA} - N_{iB})$$

$$\frac{dR_{1j}}{dt} = l_{1j}(S_{1j} - R_{1j}) - \sum_{i=1}^{4} \frac{N_{ij}}{e_{i1}} \min[c_{i1}e_{i1}R_{1j}, c_{i2}e_{i2}R_{2j}] \quad (2)$$

$$\frac{dR_{2j}}{dt} = l_{2j}(S_{2j} - R_{2j}) - \sum_{i=1}^{4} \frac{N_{ij}}{e_{i2}} \min[c_{i2}R_{2j}, c_{i1}e_{i1}R_{1j}]$$

where a is the dispersal rate. Dispersal is directional, i.e. from the community with higher density to the community with lower density (Amarasekare and Nisbet 2001). The symbols are the same as in Eq. 1 except that R_{ij}, S_{ij}, l_{ij}, and N_{ij} now refer to variables for resource i (1 or 2) in local community j (A or B). We then considered that each species had the same parameters across all local communities but each local community had a different resource supply point. This regional variation of supply points (bold line in Fig. 1) allowed different species or pairs of species to dominate in each local community. For simplicity, we used a small metacommunity consisting of 4 species (1, 2, 3 and 4) competing in two local communities (A and B). Having more species would have required more limiting resources within each community generating a multi dimensional resources space that would have added a level of complexity not necessary for the purposes of this study.

Simulations

The complexity of the equations did not allow mathematical analysis, so we instead performed numerical simulations. The parameters for each species used in the model were chosen so as to ensure a trade off between the species' competitive abilities for the two limiting resources (Fig. 1) without creating a strict symmetry in competitive abilities (parameters are given in the legend of Fig. 2). A strict symmetry would have led to a regional strict equality in the competitive abilities of all species (Mouquet and Loreau 2002), which is biologically unrealistic. Each species was initially present in all local habitats; initial species abundances (N_{ij}) were 10, and initial resource quantity was 50. We have varied the supply points of the two resources S_{1j} and S_{2j} in the two local communities along a line centered on $S_{11}=S_{12}=S_{22}=S_{21}=200$ (regional homogeneity) and bounded by $S_{11}=280$, $S_{21}=120$, $S_{12}=120$, and $S_{22}=280$ (Fig. 1). The degree of heterogeneity was measured as the distance (in resource units) between the two supply points on that line (the maximal heterogeneity is $2\times 80\sqrt{2}=226.3$). Dispersal rates has been chosen between 0.00001 and 1. For each combination of dispersal values and supply points, a simulation of Eq. 2 was run until equilibrium was reached.

Results

The relative abundances of the species in the metacommunity varied with both dispersal rate and heterogeneity; each species exhibited a different pattern of

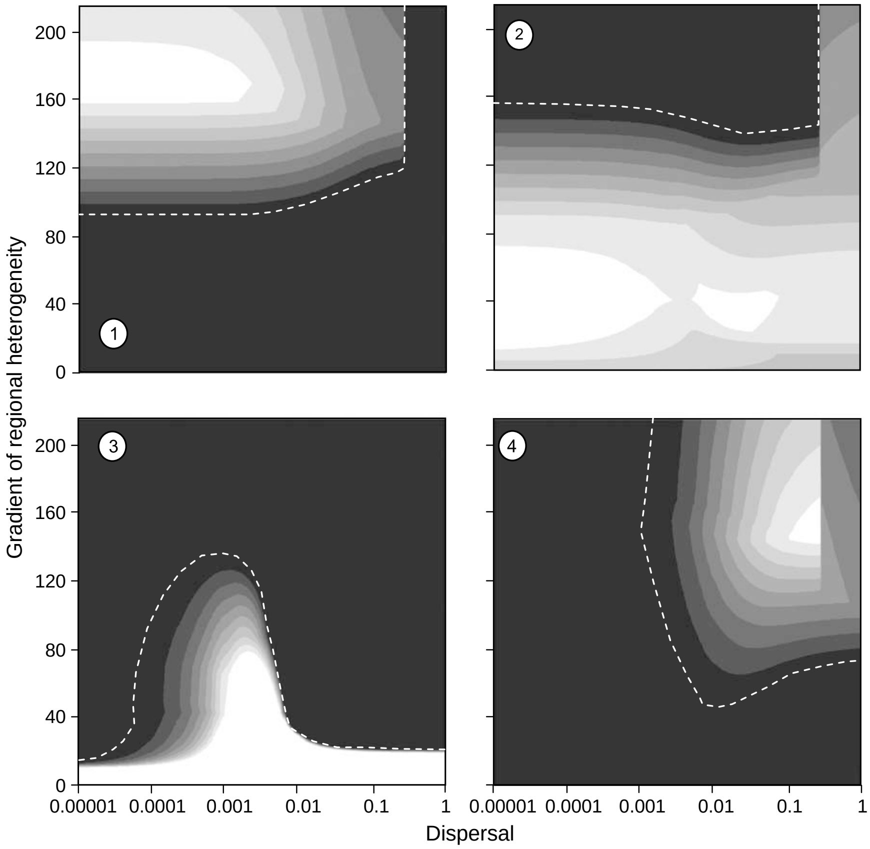

Fig. 2. Abundances at equilibrium for each species in community A for different values of dispersal and degree of heterogeneity. The parameters are as in Fig. 1, except that $c_{21} = 0.04$, $c_{22} = 0.048$ (species 2 is a better competitor at the scale of the region). The white zone corresponds to the zone of high abundances and the black zone (bounded by the broken white line) to the zone of zero abundance (we assumed a species was extinct when its abundance was lower than 1, in order to mimic the effect of stochastic extinction). Species are identified by number.

abundance (Fig. 2 illustrates abundances obtained at equilibrium in community A). Species 1 and 4, the dominant competitors for resources 1 and 2, respectively, were favored in each community at relatively high levels of heterogeneity but very different levels of dispersal. Species 2 and 3, the dominant competitors at intermediate supply rates for both resources, were favoured at relatively low levels of heterogeneity. Note that, without dispersal, species 4 never occurs in community A (it occurs in community B). The inverse is true for species 1 in community B.

Combining these patterns of abundances shows that dispersal and heterogeneity interact to determine species diversity in a metacommunity (Fig. 3). Without dispersal, no more than two species could coexist in each local community, and different species dominated at different levels of heterogeneity. Increasing dispersal to moderate rates allowed more species to coexist locally, and higher local diversity was found at intermediate levels of both dispersal and habitat heterogeneity. At higher rates of dispersal, however, diversity again decreased; some species were no longer able to persist with a regionally dominant competitor (species 2 in this simulation). Varying heterogeneity led to different levels of regional and local diversity. At low levels of regional heterogeneity, environmental conditions were the same in the two communities, and only species 2 and 3 persisted in the metacommunify. At intermediate levels of regional heterogeneity, species 1 and 2 dominated in community A, and species 3 and 4 dominated in community B. At this point, dispersal allowed for source–sink dynamics, and local diversity was high at intermediate rate of dispersal. However, too much regional heterogeneity precluded source–sink dynamics. Species 1 dominated in community A and species 4 in community B; species 2 and 3 were excluded from the metacommunity, and regional and local diversify decreased.

Discussion

Source–sink dynamics have been implicated as important in controlling metacommunity dynamics but require some level of heterogeneity among local communities (Holt 1993, Amarasekare and Nisbet 2001, Mouquet and Loreau 2002). We have defined heterogeneity as the spatial variation in resource supplies among local communities (Chase and Leibold 2003, Shurin et al. 2004) and modeled the combined effects of heterogeneity and dispersal on species abundance and diversity. As

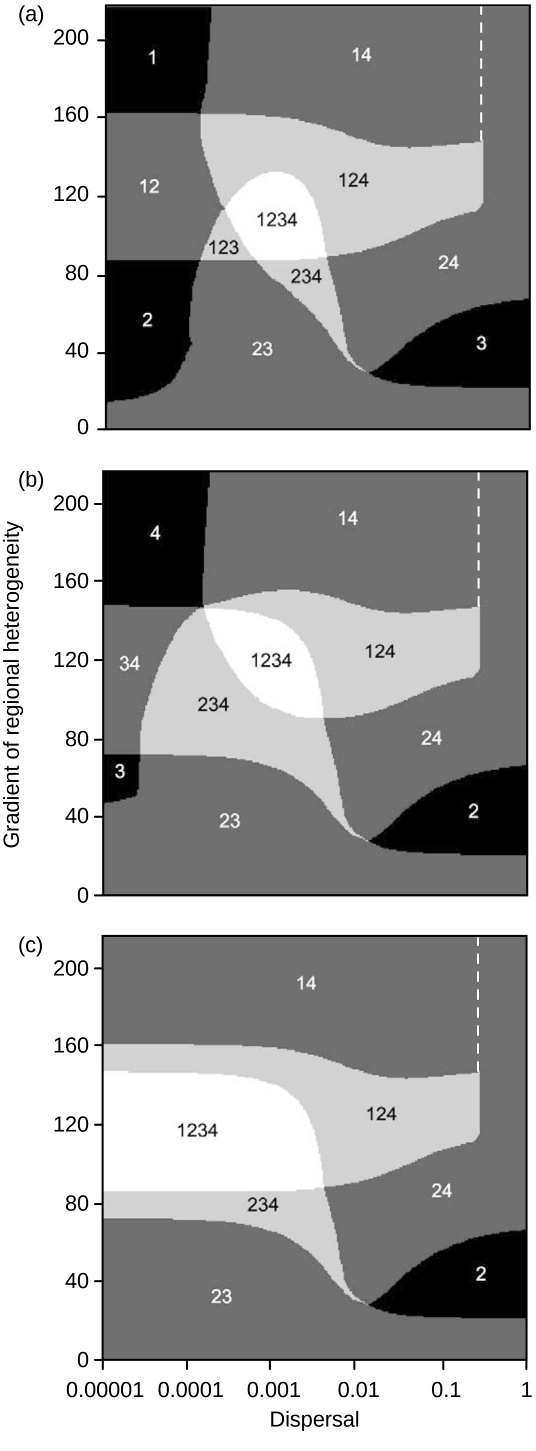

Fig. 3. Identify of the species coexisting at equilibrium (a) in community A, (b) in community B and (c) in the metacommunity, for different values of dispersal and degrees of heterogeneity. Parameters are as in Fig. 2. Species are identified by number. The local species richness is 4 in the white zones, 3 in the light grey zone, 2 in the dark grey zones and 1 in the black zone (we assumed a species was extinct when its abundance was lower than 1, in order to mimic the effect of stochastic extinction).

suggested by previous work, the highest diversify in our model is found at intermediate levels of dispersal among local communities (Mouquet and Loreau 2002, 2003, Leibold and Miller 2004), but our model provides novel insights in demonstrating the interactions between the effects of dispersal and the degree of heterogeneity among local communities (Fig. 2 and 3) and vice versa. If local communities are too similar in their resource supply points (i.e. more homogeneous), then dispersal does little to increase species diversity because no unique sources are available to any species. If local communities are too different (i.e. regional heterogeneity is too great), then dispersal again has only a small effect on diversity because differences in local competitive ability are too great and inferior competitors cannot be rescued from competitive exclusion by immigration. We found the maximal regional and local species richness when the heterogeneity between communities (the resource ratio heterogeneity) was intermediate: when it fell within a specific range of interspecific competition parameters for the pool of species considered.

Our results complement those of Codeço and Grover (2001), who found a potential for source sink dynamics along a resource gradient generated by varying the ratio between two limiting resources. Combined with their approach, our work provides a more realistic framework for modeling species competition in metacommunities and establishes a mechanistic basis for the 'intermediate difference hypothesis' – that dispersal will have its greatest effect where differences between local habitats are moderate, proposed by Kunin (1998) – with clear predictions about the joint effect of dispersal and heterogeneity in a metacommunity. Our results demonstrate that the importance of Kunin's 'intermediate difference hypothesis' will depend directly on dispersal rates (Fig. 3). A parallel can be found with models in population genetics that explain the maintenance of polymorphism in patchy environments (after Levene 1953, Gillespie 1974), where genetic diversify has been shown to be higher when the spatial correlation between patches (related to regional heterogeneity) is small and migration occurs. Ronce and Kirkpatrick (2001) showed that, in a patchy population, increasing heterogeneity, when it entails increasing the level of local maladaptation, leads to lower species density. Put in terms of species-competition outcomes, this result entails an upper limit to the regional heterogeneity at which a source–sink effect can occur, similar to that in our model.

Shurin et al. (2004) have recently proposed a metacommunity model based on spatial variation in resources supply points. They focused on the distribution of habitats along a gradient of resources with priority effects at the scale of the metacommunity. They found that abiotic heterogeneity allows local scale alternate stable equilibria and ensures regional coexistence of competitors that would otherwise exclude each other. In our model, we have not incorporated priority effects so that we could focus exclusively on the source–sink dynamics and explore the effects of a more complete range of heterogeneity. In doing that, we have shown that the distribution of each community along the resource supply points space is crucial in determining local and regional coexistence (as in Shurin et al. 2004).

Direct experimental evidence of the effects of dispersal and heterogeneity is limited, largely because of the landscape scale necessary for metacommunity experiments. The effects of dispersal on local and regional diversity in animal communities have been explored in laboratory microcosms (Warren 1996a,1996b) and natural systems (Gonzalez et al. 1998, Kneitel and Miller 2003), where generally positive effects of dispersal on diversity have been found. For plants, Shmida and Ellner (1984) showed that some annual plants were maintained solely by immigration from adjacent communities (Kadmon and Shmida 1990), but Kunin (1998) found weak evidence for mass effects in herbaceous plant communities. Experiments on heterogeneity among local habitats are even more uncommon. Cottenie et al. (2003) found significant heterogeneity in habitat conditions among interconnected ponds but no evidence of source–sink effects despite significant rates of dispersal. This result is consistent with our model: local conditions in the ponds may have been sufficiently different (regional heterogeneity may have been high enough) to preclude a mass effect. Codeço and Grover (2001) studied competition between algae and bacteria in a series of interconnected chemostats (a gradostat) with different carbon:phosphorus ratios and found higher local diversity resulting from mass effects.

Very few experiments have manipulated both dispersal and heterogeneity. Warren (1996a) created heterogeneity among local protozoan communities by disturbing (heat killing) randomly chosen local communities every three days: dispersal increased local diversify only at high disturbance rates. Forbes and Chase (2002) varied the dispersal patterns among heterogeneous zooplankton communities in artificial ponds and found no effect on local or regional diversity, but they did not manipulate heterogeneity directly. Miller, Kneitel, and Mouquet (unpubl.) have manipulated dispersal and metacommunity heterogeneity and found a combined positive effect of heterogeneity and dispersal on regional diversity but not on local diversity (local richness increased only with dispersal). Unfortunately none of the above experiments is sufficient to evaluate the 'intermediate heterogeneity and dispersal' prediction from our model. Most of these experiments use only two treatment levels for dispersal and/or heterogeneity, a practice that precludes evaluation of the pattern demonstrated in Fig. 3. More detailed factorial experiments are called for that investigate a broader set of possible community responses, but our results can provide a possible explanation for empirical studies that have not found evidence for strong source–sink or mass effects at the community level (Forbes and Chase 2002, Cottenie et al. 2003, Miller, Kneitel, and Mouquet, unpubl.). These studies may have examined communities with ranges of dispersal and regional heterogeneity too limited to reveal source–sink effects.

Our model is complementary to that previously proposed by Tilman (1982) on environmental microheterogeneity and to that previously proposed by Leibold and Chase (Leibold 1998, Chase and Leibold 2003, Shurin et al. 2004). This extension of the resource-ratio hypothesis to a regional scale (Tilman 1982, Grover 1997, Chase and Leibold 2003, Shurin et al. 2004) may provide the basis for a more mechanistic landscape ecology (Loreau et al. 2003). Concepts such as R* and resource supply points should be redefined in the context of local and regional scales (Chesson 2000b) and the

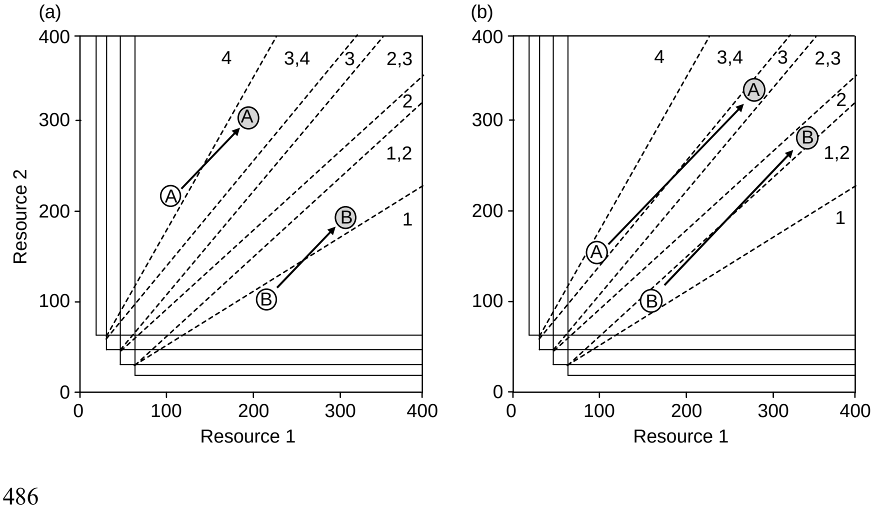

Fig. 4. Hypothetical consequences of increasing resources availability in one community of the metacommunity (based on the Fig. 1). The circles show the position of the resource supply points in community A and B prior (white) and after (gray) the resource enrichment. In (a) only two species can exist in the metacommunity prior to the resource enrichment and three or four after (depending if enrichment concerns only one or the two communities). In (b), four species coexist in the metacommunity prior to the resource enrichment and only three after.

fluxes of individuals and nutrients between adjacent communities or ecosystems. Following Tilman (1982), we can ask in such context what the consequences of resources enrichment on species richness will be. Resource enrichment could either decrease or increase species richness. If regional heterogeneity was already high prior to the resource enrichment such that only two species could coexist in the metacommunity, increasing resource supply in the metacommunity could move the resource supply ratio in regions where dispersal will allow more species to coexist locally (Fig. 4a). In contrast if regional heterogeneity was intermediate such that high local and regional diversity were maintained in the metacommunity, increasing resource supply could shift the resources supply ratio into zones where local species richness will decrease (Fig. 4b). Similar results are expected if only one community is enriched. More complex scenarios could be envisaged but this example illustrates that the scaling of resource enrichment may have important consequences metacommunity dynamics and diversity. This last point illustrates also a limit to our measure of heterogeneity since the degree of heterogeneity is the same in the two scenarios, but the consequences on species diversity are different depending of the level of resource enrichment. In our simulations, if the heterogeneity gradient had been positioned in a different area of the resource supply space, very low heterogeneity could have resulted in high local diversity as long as each community was dominated by a different set of species.

Experimental studies are now needed to help advance the more rapidly developing metacommunity theory (Holyoak et al. 2005) in particular, work that manipulates local habitat heterogeneity directly (Codeço and Grover 2001, Miller, Kneitel, and Mouquet, unpubl.) and varies the spatial distribution of local habitat types (Snyder and Chesson 2003, Shurin et al. 2004).

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References

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

Amarasekare, P. and Nisbet, R. M. 2001. Spatial heterogeneity, source–sink dynamics and the local coexistence of competing species. – Am. Nat. 158: 572–584.

Chase, J. M. and Leibold, M. A. 2003. Ecological niches. Linking classical and contemporary approaches. – Univ. of Chicago Press.

Chesson, P. L. 2000a. General theory of competitive coexistence in spatially-varying environments. – Theor. Popul. Biol. 58: 211–237.

Chesson, P. 2000b. Mechanisms of maintenance of species diversity. – Annu. Rev. Ecol. Syst. 31: 343–366.

Codeço, C. T. and Grover, J. P. 2001. Competition along a spatial gradient of resource supply: a microbial experiment model. – Am. Nat. 157: 300–315.

Cottenie, K., Michels, E., Nuytten, N. et al. 2003. Zooplankton metacommunity structure: regional versus local processes in highly interconnected ponds. – Ecology 84: 991–1000.

Forbes, A. E. and Chase, J. M. 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. – Oikos 96: 433–440.

Gillespie, J. 1974. Polymorphism in patchy environments. – Am. Nat. 108: 145–151.

Gonzalez, A., Lawton, J. H., Gilbert, F. S. et al. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. – Science 281: 2045–2047.

Grover, J. P. 1997. Resource competition. – Chapman and Hall.

Holyoak, M., Leibold, M. A. and Holt, R. 2005. Metacommunities: spatial dynamics and ecological communities. – Chicago Univ. Press.

Holt, R. D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. – In: Ricklefs, R. E. and Schluter, D. (eds), Species diversity in ecological communities: historical and geographical perspectives. Univ.of Chicago Press, pp. 77–88.

Kadmon, R. and Shmida, A. 1990. Spatiotemporal demographic processes in plant populations: an approach and a case study. – Am. Nat. 135: 382–397.

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

Kneitel, J. M. and Chase, J. M. 2004. Trade offs in community ecology: linking spatial scales and species coexistence. – Ecol. Lett 7: 69–80.

Kunin, W. E. 1998. Biodiversity at the edge: a test of the importance of spatial 'mass effects' in the Rothamsted Park grass experiments. – Proc. Natl Acad. Sci USA 95: 207–212.

Leibold, M. A. 1998. Similarity and local co-existence of species in regional biotas. – Evol. Ecol. 12: 95–110.

Leibold, M. A. and Miller, T. E. 2004. From metapopulations to metacommunities. – In: Hanski, I and Gaggiotti, O. E. (eds), Ecology, genetics, and evolution of metapopulations. Elsevier Academic Press, pp. 133–150.

Leibold, M. A., Holyoak, M., Mouquet, N. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – Ecol. Lett 7: 601–613.

Leon, J. A. and Tumpson, D. B. 1975. Competition between two species for two complementary or substitutable resources. – J. Theor. Biol. 50: 185–201.

Levene, H. 1953. Genetic equilibrium when more than one ecological niche is available. – Am. Nat. 87: 331–333.

Levin, S. A. 1974. Dispersion and population interactions. – Am. Nat. 108: 207–228.

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

Loreau, M., Mouquet, N. and Holt, R. 2003. Meta-ecosystem: a framework for a spatial ecosystem ecology. – Ecol. Lett. 6: 673–679.

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

Mouquet, N. and Loreau, M. 2002. Coexistence in metacommunities: the regional similarity hypothesis. – Am. Nat. 159: 420–426.

Mouquet, N. and Loreau, M. 2003. Community patterns in source–sink metacommunities. – Am. Nat. 162: 544–557.

Pulliam, H. R. 2000. On the relationship between niche and distribution. – Ecol. Lett. 3: 349–361.

Ronce, O. and Kirkpatrick, M. 2001. When sources become sinks: migrational meltdown in heterogeneous habitats. – Evolution 55: 1520–1531.

Shmida, A. and Ellner, S. 1984. Coexistence of plant species with similar niches. – Vegetatio 58: 29–55.

Shurin, J. B., P. Amarasekare, J. M., Chase, R. D. et al. 2004. Alternative stable states and regional community structure. – J. Theor. Biol. 227:359–368.

Snyder, R. E. and Chesson, P. 2003. Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. – Ecol. Lett. 6: 301–309.

Tilman, D. 1982. Resource competition and community structure. – Princeton Univ. Press.

Warren, P. H. 1996a. Dispersal and destruction in a multiple habitat system: an experimental approach using protist communities. – Oikos 77: 317–325.

Warren, P. H. 1996b. The effects of between-habitat dispersal rate on protist communities and metacommunities in microcosms at two spatial scales. – Oecologia 105: 132–140.

Wilson, D. S. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. – Ecology 73: 1984–2000.