

Factors controlling community structure in heterogeneous metacommunities

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Summary

1. Modern theories of species coexistence recognize the importance of environmental heterogeneity.
2. Despite the existence of many observational studies, few experimental studies have evaluated the extent to which, and mechanisms by which, fixed spatial heterogeneity increases community diversity and alters community structure.
3. In experimental protist communities, we found that non-spatial mechanisms unrelated to heterogeneity were responsible for a large component of baseline diversity. Above this baseline, fixed spatial heterogeneity produced small but predictable increases in metacommunity diversity through species sorting, while heterogeneity and dispersal together altered local community structure (composition and relative abundance) through mass effects.
4. Our study illustrates that heterogeneity is not always the strongest driver of diversity, while experimentally demonstrating mechanisms by which heterogeneity alters community structure.

Key-words: dispersal, diversity, metacommunity, protozoa, spatial heterogeneity

Introduction

A fundamental aim of ecology is to understand what determines the biodiversity of ecological communities. Niches provide one of the oldest and most influential explanations for the coexistence of species (Elton 1927; Hutchinson 1957; MacArthur 1958; Chesson 1991). We have long known that niches promote coexistence. This can occur through variation in resource use (e.g. Tilman's R^* rule, Tilman 1982), including trophic specialization opportunities arising from community complexity (Elton 1927), or through spatial (e.g. MacArthur 1958) or temporal (e.g. Pianka 1969) division of apparently homogeneous habitats within a local community. Spatial niche division can also take more complex forms at larger spatial scales in homogeneous habitats, such as through among-species trade-offs in the rates of competition and colonization (Hastings 1980; Tilman 2004). However, there has been little experimental examination of how heterogeneity at above-community (metacommunity) spatial scales influences diversity.

There are different types of heterogeneity (Melbourne *et al.* 2007). An important distinction is between environmental or abiotic heterogeneity vs. biotic heterogeneity. Environ-

mental heterogeneity is variation in the physical environment, whereas biotic heterogeneity is variation in the occurrence and abundance of organisms. The focus of this paper is environmental heterogeneity. A second distinction is between temporal, spatial and spatiotemporal heterogeneity. Temporal heterogeneity is the tendency for locations within an area to fluctuate in unison. Weather, particularly temperature, is a good example of temporal heterogeneity. Fixed spatial heterogeneity is the tendency for the heterogeneity among locations to remain fixed through time; spatial heterogeneity of nutrient resources derived from parent bedrock is a good example. Combined spatiotemporal heterogeneity is the result of adding temporal, spatial and pure spatiotemporal heterogeneity together. Many types of disturbance are good examples of pure spatiotemporal heterogeneity because the timing and location of disturbances are random. Here our focus is fixed spatial heterogeneity.

Fixed spatial heterogeneity is prevalent in nature, and includes topographical, micro-topographical and environmental gradients in resources, as well as patchiness in soil nutrients. Theory is well developed to illustrate potential mechanisms by which more species can coexist in spatially heterogeneous environments than spatially homogeneous ones (Chesson 2000b; Amarasekare 2003; Chase *et al.* 2005; Mouquet, Hoopes & Amarasekare 2005). Previous experimental studies of the effects of spatial heterogeneity on community structure have most often focused on spatiotemporal

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heterogeneity, in particular, the effects of disturbance (Warren 1996; Gaston & Warren 1997; Kneitel & Chase 2004; Ostman, Kneitel & Chase 2006; Cadotte 2007a, b; Haddad *et al.* 2008; Questad & Foster 2008).

Some excellent studies have manipulated fixed spatial heterogeneity (and other factors) in interconnected habitats (Kneitel & Miller 2002, 2003; Cadotte, Fortner & Fukami 2006; Fox 2007) but because they did not contrast the effect of fixed spatial heterogeneity with homogeneous controls, it is not possible to attribute effects on community structure to fixed spatial heterogeneity *per se*. Fixed spatial heterogeneity provides some of the most robust hypotheses for diversity maintenance; however, few studies have experimentally tested for the effects of fixed spatial heterogeneity on community structure by comparing heterogeneous metacommunities with control homogeneous metacommunities (Vivian-Smith 1997; Collins & Wein 1998; Stevens & Carson 2002; Baer *et al.* 2004; Holt, Warren & Gaston 2004; Reynolds *et al.* 2007).

Considering the effects of fixed spatial heterogeneity in a metacommunity context also requires focusing on dispersal. The mechanisms that underlie the effect of heterogeneity and dispersal on community structure can be interpreted in the context of a metacommunity framework (Leibold *et al.* 2004; Holyoak, Leibold & Holt 2005). The mechanisms proposed by Chesson (2000a) can also be aligned with this framework (Melbourne *et al.* 2007). The metacommunity framework provides a context for understanding the effects of dispersal and fixed spatial heterogeneity on metacommunity and community structure. Here we focus on the three niche-based paradigms: species sorting, patch dynamics and mass effects. These paradigms include all three types of heterogeneity.

First, spatiotemporal niches can occur in homogeneous environments, through *patch dynamics*, when species have tradeoffs between traits such as competitive ability and either colonization ability (Hastings 1980) or the ability to withstand predators (Paine 1966). Hence, coexistence is possible in homogeneous environments. Second *species sorting* recognizes that important environmental drivers, such as temperature, water, nutrients and sunlight, vary in space and time and that this creates opportunities for different species to occupy different habitats if they can reach them (Chase & Leibold 2003). Third, if dispersal is frequent, species may segregate into habitats but be redistributed by a *mass effect*, the flow of individuals between good and poor habitats (Amarasekare & Nisbet 2001; Mouquet & Loreau 2003). Source-sink models are a special case of mass effects, where populations in poor environments have negative finite growth rates and are frequently supplemented via immigration from good environments (Pulliam 1988). In comparison, mass effects can have low rather than negative growth rates in poor environments. Under fixed spatial heterogeneity, we expect species sorting and mass effects to be potentially important mechanisms underlying patterns of richness and species composition.

Using protists in experimental microcosms, we (i) tested for effects of fixed spatial heterogeneity and dispersal on

metacommunity structure; and (ii) aimed to determine the mechanisms underlying differences in community structure between homogeneous and heterogeneous metacommunities. We predicted that diversity would be greater in heterogeneous metacommunities than homogeneous metacommunities, and that the composition and relative abundance of species would differ between heterogeneous and homogeneous metacommunities. We also predicted that we should find evidence of species sorting and mass effects. Microcosm experiments represent a part of the continuum between purely theoretical models and large-scale unmanipulable but natural metacommunities. Compared to models they offer replication and real biology and ecology, but compared to natural systems in the field they have a reduced level of complexity. Importantly, for our purposes, they permit the control of issues of spatial scale, in a system uncomplicated by immigration of species from outside of the putative metacommunity, and provide many generations of data from a system with trophic structure (Lawton 1995; Srivastava *et al.* 2004).

Material and methods

To manipulate dispersal and resource heterogeneity among local communities, we created arenas for microbial metacommunities by connecting arrays of nine 100-mL bottles with tubing (Fig. 1). We examined the role of dispersal by comparing these metacommunities to groups of isolated 100-mL bottles, with no dispersal between local communities (Fig. 1). We created resource heterogeneity within metacommunities by placing either wheat seeds (five bottles) or leaf litter (four bottles) in alternate bottles. We created spatially homogeneous metacommunities by placing 'mixed resources' consisting of both wheat seeds and leaf litter in each bottle in equivalent total amounts to the heterogeneous metacommunities (there is resource heterogeneity within local communities but resources are homogeneously distributed in space). Wheat seeds, leaf litter and mixed resources were contained in ultra fine polypropylene mesh bags of identical size. Thus, both resource types provided the same amount of physical habitat heterogeneity within bottles. There were five replicates of each community type.

Initial communities consisted of 25 species, including autotrophic producers, mixotrophs, herbivores, bacterivores and predators (Table S1), from a pond community in New Jersey, USA (McGrady-Steed, Harris & Morin 1997). Five species went extinct from all treatments within 10 weeks, leaving 20 species in experimental communities. After addition of bacterized nutrient medium, we temporally staggered species addition to ensure that prey (bacterivores, autotrophs and omnivores) became abundant before predators were added. After 10 weeks, the population density of each species was determined by counting the number of individuals in a given volume. We also sampled presence and absence after 4 and 8 weeks, and these data confirm the results for abundance presented here (K. F. Davies, unpublished data). After mixing, we took a single sample of 10 mL from each 100-mL bottle. As the experiment was large in size, we sampled three bottles from homogeneous metacommunities and the first five bottles from heterogeneous metacommunities (giving one bottle of each distinct resource and tube-number combination). However, for our statistical tests, only three bottles each from heterogeneous metacommunities and homogeneous metacommunities were compared. For heterogeneous metacommunities, these included two

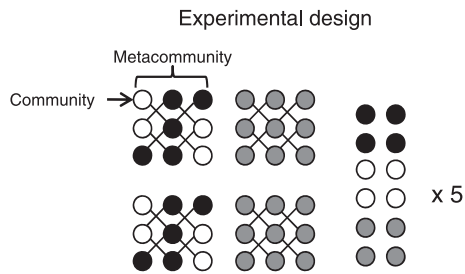


Fig. 1. Experimental design. Black = wheat, white = leaf, grey = mixed resources. Circles represent 100-mL communities, and lines represent tubes that connect communities in metacommunities.

leaf bottles and one wheat bottle – this was a more conservative combination than two wheat bottles and one leaf bottle because most species were more abundant in wheat bottles. (We also compared ‘two wheat, one leaf’ combinations with homogeneous metacommunities and these consistently gave us stronger effects and lower P -values than the ‘two leaf, one wheat’ combination.) For comparisons with groups of isolated bottles without dispersal between local communities, we compared three randomly selected isolated bottles of the appropriate combination: three mixed resource bottles for homogeneous control metacommunities, and two leaf bottles and one wheat bottle for heterogeneous control metacommunities.

Sterile technique was used throughout the experiment. Bacteria added consisted of *Serratia marcescens*, *Bacillus subtilis* and *Enterobacter aerogenes*, all of which were obtained from Carolina Biological Supply Co. (Burlington, NC, USA). Nutrient medium consisted of soil, protozoan pellets (Carolina Biological Supply Co.) and water (McGrady-Steed *et al.* 1997), and was bacterized 24 hours before protist species were added. Other organisms listed in Table S1 were added at a constant number per unit volume to all microcosms. Weekly replacement of 10% of the medium in each bottle provided supplemental nutrients.

Protists were sampled in varying volumes depending on the species. *Euglena* and diatoms were enumerated by censusing fields of a Sedgwick rafter (algal counting) chamber under a compound microscope at 400 \times magnification. Counts of transects of the rafter chamber were used to enumerate *Ankistrodesmus* sp., round alga sp., *Chlamydomonas* sp., *Scenedesmus* sp., *Staurastrum* sp., *Uronema* sp. and *Cyclidium* sp. If fewer than eight individuals of these species were found in transects of the whole rafter chamber (1 mL total), we searched larger volumes up to 3 mL under a binocular microscope with dark-field illumination at magnifications of up to 120 \times . Precise volumes censused under the binocular microscope were determined by weight. Those species not listed above were larger and were counted in the entire 10-mL sample using the binocular microscope.

We used the analysis of variance (ANOVA; Genstat Version 9.1; VSN International Ltd, Hemel Hempstead, UK) to test for differences in species richness. First, we tested for a difference in the richness of homogeneous and heterogeneous metacommunities, and local communities within metacommunities. For these tests, we considered only metacommunities (that is, with dispersal). Second, to understand how heterogeneity and dispersal affected metacommunity and community richness, we used ANOVA to test for an effect of heterogeneity, dispersal and their interaction, at both metacommunity and local scales. For these tests, we considered both metacommunities and groups of unconnected bottles. Third, we used ANOVA to look for differences in richness in isolated bottles with leaf, wheat and mixed resources. Finally, we used ANOVA to test for the effect of different resources (wheat and leaf) on individual species' abundances. We

looked both at communities connected in metacommunities and at isolated communities.

We then repeated the above analyses, this time testing for differences in species composition and relative abundance. For these tests, we used non-metric multidimensional scaling (implemented in R; R Development Core Team 2007) to investigate the dissimilarity in composition and abundance using the Bray–Curtis measure of dissimilarity (Bray & Curtis 1957). For all of these comparisons of community composition and relative abundance, we used the analysis of similarity (ANOSIM) to test for the significance of differences.

Results

NON-SPATIAL DYNAMICS

Non-spatial dynamics played a large role in baseline diversity as is illustrated by isolated local communities. Baseline diversity within bottles ranged from *c.* 12 to 14 species depending on resource type (Fig. 2a). Leaf-only bottles contained the most species-poor communities (Fig. 2a). In addition to the difference in diversity between resource types, composition and abundance were also different between isolated leaf and isolated wheat communities ($P = 0.01$, Bray–Curtis dissimilarity).

EFFECTS OF FIXED SPATIAL HETEROGENEITY ON METACOMMUNITY STRUCTURE

Consistent with fixed spatial heterogeneity influencing diversity, spatially heterogeneous metacommunities were more diverse regionally than homogeneous metacommunities [Fig. 2b; $P = 0.05$; standard error of difference (SED) = 0.50] but on average by only one species, or 7%. These differences were driven by the community membership of two species. ‘Small *Amoeba*’ was a member of heterogeneous metacommunities but never occurred in homogeneous metacommunities, and *Staurastrum* sp. was a member of heterogeneous metacommunities but was represented by just two individuals in only one homogeneous metacommunity. Species composition and relative abundance of heterogeneous and homogeneous metacommunities also differed significantly ($P = 0.038$). However, at the local scale, the diversity of local communities in heterogeneous and homogeneous metacommunities was not significantly different (mean for heterogeneous 14.0, homogeneous 13.8; $P = 0.38$; SED = 0.27).

EFFECTS OF DISPERSAL, FIXED SPATIAL HETEROGENEITY, AND THEIR INTERACTION ON METACOMMUNITY STRUCTURE

At the regional scale, only heterogeneity affected species richness (Fig. 2c; Table 1). Dispersal and the interaction between heterogeneity and dispersal had no effect (Table 1). The findings in composition and abundance mirrored the richness result, with only a significant effect of heterogeneity on composition and abundance ($P = 0.02$) but no effect of dispersal

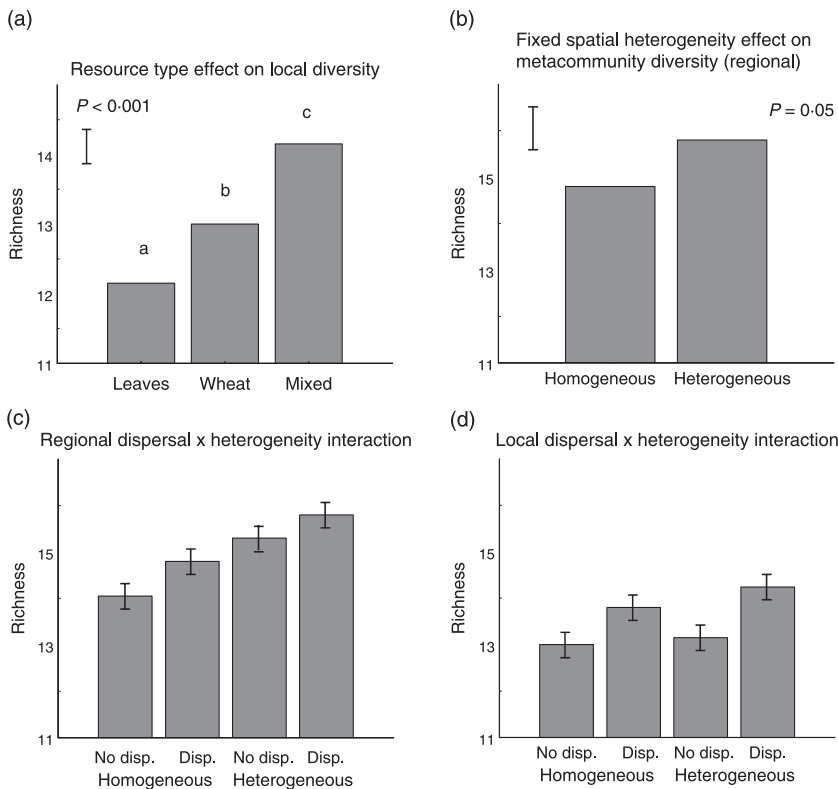


Fig. 2 (a) Mean protist local diversity in different resource types: leaves, wheat and mixed (leaves plus wheat) resources. Comparisons were made for isolated bottles. The bar represents two times the standard error of the difference. (b) Mean protist diversity in heterogeneous vs. homogeneous metacommunities at the regional scale. The bar represents two times the standard error of the difference. (c) Effect of fixed spatial heterogeneity and dispersal on regional protist diversity. Error bars represent standard deviations. (d) Effect of fixed spatial heterogeneity and dispersal on local protist diversity. Error bars represent standard deviations.

Table 1. ANOVA of the effects of fixed spatial heterogeneity and dispersal on regional richness

Source of variation	d.f.	SS.	MS	VR	<i>P</i>
Block stratum	4	20.000	5.000	4.19	
Units stratum					
Heterogeneity	1	12.100	12.100	10.14	0.003
Dispersal	1	3.600	3.600	3.02	0.092
Heterogeneity × dispersal	1	0.100	0.100	0.08	0.774
Residual	32	38.200	1.194		
Total	39	74.000			

d.f., degrees of freedom; SS, sum of squares; MS, mean squares; VR, variance ratio.

($P = 0.08$). Because we were not able to test for an interaction term using ANOSIM, we performed two additional analyses. We looked for an effect of dispersal in homogeneous metacommunities, that is, with and without dispersal. We found no effect ($P = 0.14$).

At the local scale, only dispersal affected species richness (Fig. 2d; dispersal, $P < 0.001$; heterogeneity, $P = 0.82$; dispersal × heterogeneity, $P = 0.85$). Similarly, only dispersal affected composition and abundance (dispersal, $P < 0.001$; heterogeneity, $P = 0.55$). Again, for composition and abundance, we performed the same additional analyses as we did for regional data to explore the interaction. While dispersal had no effect in homogeneous metacommunities, it had an effect in heterogeneous metacommunities. Composition and abundance ($P < 0.001$; Fig. 3) were significantly different in local communities in heterogeneous metacommunities con-

nected by dispersal than in local communities not connected by dispersal. Further, isolated leaf communities were distinct in composition and abundance from leaf communities in metacommunities, isolated wheat communities and wheat communities in metacommunities (Fig. 3). In other words, metacommunity connections altered the composition and relative abundance of species in local leaf communities. Leaf communities connected in metacommunities were intermediate in composition and abundance between isolated leaf and connected and isolated wheat communities. By comparison, isolated and connected wheat communities did not separate in multivariate space (Fig. 3). Hence, although wheat communities influenced leaf communities in metacommunities, leaf communities did not affect wheat communities.

RESOURCE EFFECTS ON INDIVIDUAL SPECIES

Twelve of 15 species were significantly more abundant in either wheat or leaf resources in isolated bottles, indicating that most species had a resource preference. Nine of those 12 species were significantly more abundant in their unfavoured resource in heterogeneous metacommunities with dispersal possible than in isolated bottles of the same resource type, suggesting that abundance was boosted by dispersal from bottles containing the preferred resource (Table S2). Two prey species were less abundant in their favoured resource in metacommunities than in isolated bottles of the same resource type. Finally, three species that had no preference for leaf or wheat resources were equally abundant on a given resource in isolated bottles compared with bottles of the same resource in metacommunities.

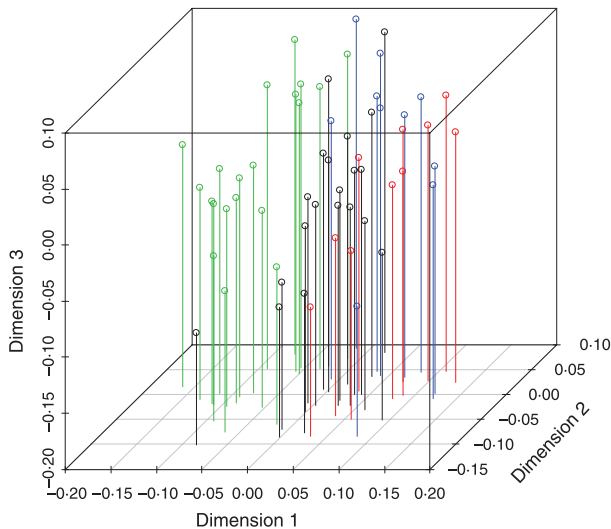


Fig. 3. Visual representation in three-dimensional ordination space of the dissimilarity in species composition and relative abundance in bottles in heterogeneous and homogeneous metacommunities, from non-metric multidimensional scaling (Bray–Curtis dissimilarity, ANOSIM $P < 0.001$). Isolated leaf communities were distinct from leaf communities in metacommunities (connected), and isolated wheat communities and wheat communities in metacommunities. Connected leaf communities were intermediate between isolated leaf and connected and isolated wheat communities. Isolated and connected wheat communities did not separate in ordination space suggesting that being connected in metacommunities did not alter wheat communities. Key: connected leaf communities (black), connected wheat communities (red), isolated leaf communities (green), isolated wheat communities (blue). Note that isolated leaf communities (green) clearly separate from all other treatments.

Discussion

EFFECTS OF FIXED SPATIAL HETEROGENEITY ON METACOMMUNITY STRUCTURE

Fixed spatial heterogeneity produced modest increases in metacommunity diversity by overcoming competitive exclusion observed in homogeneous metacommunities. Diversity was increased, on average, by *c.* 7% (Fig 2b). This difference was accounted for by the community membership of two species, which were excluded from homogeneous metacommunities. Although the difference in overall diversity was small, the effect of heterogeneity on metacommunities was strong in the sense that complete exclusion of two species was reversed by heterogeneity. That is, fixed spatial heterogeneity of resources ultimately allowed two additional species to coexist with the rest of the community, whereas these species were excluded from communities in homogeneous environments. Further, this result was obtained with the introduction of minimal heterogeneity, a single level of just two resources, in contrast to nature where we see heterogeneity in multiple resources across a range of resource levels. In addition to changes in community diversity, fixed spatial heterogeneity created differences in the composition and abundance of species in heterogeneous vs. homogeneous metacommunities.

Most species were more abundant in heterogeneous metacommunities than in homogeneous metacommunities.

There are relatively few experimental studies of the effects of fixed spatial heterogeneity on community structure. Holt *et al.* (2004) directly manipulated fixed spatial heterogeneity; however, its effects on community structure were not the focus of their study. They examined how fixed spatial heterogeneity affected the form of the interspecific relationship between the abundance and occupancy of species. This relationship tends to be positive within taxonomic assemblages, with species with low local abundances tending to be restricted in distribution, and species with high local abundances more widely distributed. Holt *et al.* (2004) found that heterogeneity did not alter the importance of interactions between species in creating this positive relationship. Several other microcosm studies manipulated fixed spatial heterogeneity, together with factors like dispersal, disturbance and predator density, but they did not include homogeneous controls (Kneitel & Miller 2002, 2003; Kneitel & Chase 2004; Cadotte *et al.* 2006). In these studies, local diversity generally increased with resource level. We cannot make strong inferences about the effects of fixed spatial heterogeneity *per se* on metacommunity structure from these studies because of the lack of homogeneous controls. A handful of plant studies manipulated fixed spatial heterogeneity and made comparisons with homogeneous controls. Most of these studies did not detect an affect of heterogeneity on diversity (Collins & Wein 1998; Stevens & Carson 2002; Baer *et al.* 2004; Reynolds *et al.* 2007) probably because the dominant clonal species, including grasses, integrated resource use across patch types, using homogeneous and heterogeneous habitats in a similar way (Baer *et al.* 2004; Reynolds *et al.* 2007). One plant study detected an increase in the richness of freshwater wetland communities with microtopographic heterogeneity compared to those without (Vivian-Smith 1997). However, this study did not examine the effects of heterogeneity in isolation because adding topography also added more types of habitat; if more habitat types are available, we should expect more species to coexist. In comparison, our study contrasts the same types (leaf and wheat) and quantity of habitat in both homogeneous and heterogeneous treatments; only the spatial distribution of the resources differed between treatments.

Our study showed that fixed spatial heterogeneity altered metacommunity structure, by increasing diversity and altering composition and abundance. This is an important experimental result given the emphasis on fixed spatial heterogeneity in coexistence theory and the prevalence of fixed spatial heterogeneity in the natural world. Nonetheless, the effects of fixed spatial heterogeneity on total metacommunity richness were not large and non-spatial mechanisms were more important in determining richness.

NON-SPATIAL MECHANISMS

Non-spatial mechanisms such as classical niche partitioning unrelated to heterogeneity (Hutchinson 1957; MacArthur

1958; Chase & Leibold 2003) were responsible for a large component of baseline diversity of our local communities. The increase in diversity attributable to fixed spatial heterogeneity with dispersal in metacommunities was only about two to four species greater than the diversity of isolated bottles (Fig. 2b vs. 2a). The high baseline diversity is perhaps not surprising given the relatively complex trophic structure of the communities, which should provide many local niche opportunities that do not rely on spatial processes. This mirrors both traditional niche theories of diet specialization (Grinnell 1917; Elton 1927) as well as dynamical theories related to the strength of trophic interactions (McCann, Hastings & Huxel 1998) or food-web arrangement (Allesina, Alonso & Pascual 2008). However, it raises, more generally, the question of the importance of spatial mechanisms over non-spatial mechanisms.

METACOMMUNITY MECHANISMS

Fixed spatial heterogeneity alone, not dispersal, drove the difference in diversity between heterogeneous and homogeneous metacommunities, suggesting that species sorting (Chase & Leibold 2003; Leibold *et al.* 2004) played a dominant role in the increased diversity of heterogeneous metacommunities. Two treatment comparisons illustrate the importance of species sorting. First, regional diversity was increased in heterogeneous metacommunities compared to homogeneous metacommunities. This demonstrates that the addition of spatial heterogeneity increased diversity, as required by species sorting (Chase & Leibold 2003; Leibold *et al.* 2004). Second, regional diversity was not increased in heterogeneous metacommunities with dispersal compared to heterogeneous groups of isolated bottles with no dispersal. In other words, dispersal in heterogeneous metacommunities did not alter diversity, suggesting that coexistence mechanisms requiring more dispersal than species sorting were not involved at this scale.

In species sorting, different environments favour different species so that the better competitor on a single resource outcompetes other species and 'wins' on that resource (Chase & Leibold 2003; Leibold *et al.* 2004). We initiated our local communities by adding all species to all patches. Therefore, in isolated patches, the species favoured by the environment of that patch (leaf or wheat) should outcompete the non-favoured species, and species will be sorted among patch types. Joining up patches to allow dispersal has two possible outcomes. First, dispersal merely allows species to find their favoured patch type and outcompete non-favoured species in that patch type (species sorting). Then, as we found, there will be no additional effect of dispersal on regional diversity compared to isolated patches inoculated with all species. The second, alternative, outcome is that dispersal provides opportunities for species to boost their regional fitness through spatial subsidies to less-favoured patch types (mass effects), enhancing coexistence (Amarasekare & Nisbet 2001; Mouquet & Loreau 2003; Leibold *et al.* 2004). Then, regional diversity will be further increased by the combined effect of

dispersal and spatial heterogeneity of the environment. As we did not observe a further effect of dispersal on diversity over and above the effect of heterogeneity alone, we conclude that species sorting was the dominant mechanism leading to increased diversity of metacommunities at the regional scale. Regionally, we can rule out a role for patch dynamics (Hastings 1980; Leibold *et al.* 2004) and mass effects (Amarasekare & Nisbet 2001; Mouquet & Loreau 2003; Leibold *et al.* 2004) in the greater diversity (species richness) of heterogeneous metacommunities because of the lack of an effect of dispersal.

At the local scale, both dispersal and fixed spatial heterogeneity affected community structure, including effects on local diversity, composition and abundance. Dispersal between local communities increased the diversity of local communities in heterogeneous metacommunities (Fig. 2d). Mass effects (Amarasekare & Nisbet 2001; Mouquet & Loreau 2003; Leibold *et al.* 2004) were likely responsible, with populations in poor habitat patches being supplemented with individuals from good habitat patches through dispersal. Two lines of evidence support this conclusion: the responses of individual species (Table S2), and a dissimilarity analysis of composition and abundance (Fig. 3). We discuss these lines of evidence in turn.

First, for individual species, mass effects are indicated by boosted abundances in bottles of poor, or sink, habitat within heterogeneous metacommunities vs. isolated bottles of the same habitat (Table S2). This suggests that abundances were boosted in sink habitat from the flow of individuals moving from good habitat to poor habitat. In contrast, three species with no resource preference showed no evidence of a dispersal subsidy, that is, no mass effect.

Second, these changes in the abundance of individual species translated into local scale differences in composition and abundance between isolated and connected metacommunities (Fig. 3). However, only the relative abundance of species in local leaf communities was altered. That is, wheat communities influenced leaf community structure in metacommunities but leaf communities did not influence wheat communities.

Finally, although mass effects were present at the local scale, their effects did not translate into changes in metacommunity structure at the regional scale. To illustrate how this is possible, consider a two-patch, two-species system with one species persisting in each patch locally. Then regional diversity would be two and local diversity would be one. If mass effects were present so that each species dispersed into the other patch but did not drive the other species extinct, then regional diversity would still be two but local diversity would now also be two, thus demonstrating that mass effects can alter local but not regional diversity.

Our findings are in line with recent non-experimental studies in which species sorting and mass effects were considered important mechanisms in species coexistence in heterogeneous environments. Cottenie (2005) surveyed species composition in 158 community data sets and found that habitat variables were more important than dispersal

between communities (attributed to species sorting). Similarly, both species sorting and mass effects were suggested to play roles in structuring freshwater pond metacommunities in Connecticut (Urban 2004). Mass effects were implicated in bat metacommunities in Paraguay (Stevens, Lopez-Gonzalez & Presley 2007). Finally, in an experimental study, Questad & Foster (2008) created spatiotemporal heterogeneity in grasslands and demonstrated a role for species sorting in community-scale coexistence. These studies consider heterogeneity in a general sense. Theory suggests that different kinds of heterogeneity should have different effects on coexistence (Chesson 2000a). Thus experiments manipulating heterogeneity in specific ways are needed. By isolating the effects of fixed spatial heterogeneity from heterogeneity generally, we show that species sorting arises through fixed spatial heterogeneity.

In summary, our goal was to experimentally test for the effect of fixed spatial heterogeneity on metacommunity structure, and determine the mechanisms underlying differences in community structure. In experimental protist communities, non-spatial mechanisms, like classic niche partitioning, were responsible for a large component of baseline diversity. Fixed spatial heterogeneity modestly increased metacommunity diversity at regional scales through species sorting, while heterogeneity and dispersal together altered local community structure (composition and relative abundance) through mass effects.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Species included in experimental protist communities

Table S2. Evidence for mass effects: responses of individual species

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