

## The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities

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Theory predicts that inter-patch dispersal rates and patterns of patch heterogeneity both have the potential to alter patterns of local and regional species diversity. To test this, we manipulated both rates of habitat connectivity and the geometric arrangement of habitat heterogeneity within regions of experimental zooplankton communities. We found no effects of habitat geometry on any metric of species diversity or composition. Additionally, we found no effect of habitat connectivity rate on local species diversity. We did, however, find that increasing connectivity led to a decrease in regional diversity, as well as an increase in the percent similarity of local communities within regions. Of all of the species in these communities, the relatively large cladoceran *Ceriodaphnia reticulata* significantly responded to the treatments, and had a higher probability of achieving high densities when connectance was high. As such, we suggest that this species played a large role in driving the increased local community similarity and decreased regional species richness as connectivity increased. These findings are in opposition to previous experimental studies of metacommunities, but support the notion that increased connectance among local patches may decrease regional diversity when patches are heterogeneous.

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Traditionally, community ecology has focused on processes acting locally to determine species composition within a local habitat patch. However, recent theoretical and empirical studies have focused on the additional impact of regional processes upon local dynamics (Ricklefs 1987, Ricklefs and Schluter 1993, Holt 1997, Tilman 1997, Harrison 1999, Huston 1999, Shurin 2000, Hubbell 2001). When dispersal connects local communities to form a metacommunity (an assemblage of species persisting in a series of interconnected habitat patches), both local and regional processes can play a role in determining structure, diversity and composition at local and regional scales (Ricklefs 1987, Harrison 1999, Amarasekare 2000, Taneyhill 2000, Mouquet and Loreau 2002). Local processes include species interactions as well as possible subpopulation extinctions, whereas regional processes include rates of immigra-

tion/emigration between local communities, and the spatial arrangement of heterogeneous patches.

Studies have suggested that connections among local patches can increase local diversity levels through a variety of mechanisms. These include: (1) spatial rescue effects (Brown and Kodric-Brown 1977, Hanski 1999), where colonists from other patches rescue subpopulations that have gone extinct (or prevent local extinctions); (2) enhanced coexistence through spatial refuges from species interactions such as competition or predation (Horn and MacArthur 1972, Hastings 1980, Tilman 1994, Holyoak and Lawler 1996, Chesson 2000), where spatial processes allow coexistence of species that differentially colonize and go extinct from habitats; and (3) source-sink effects (Loreau and Mouquet 1999, Amarasekare and Nisbet 2001), where spatial connectivity potentially increases coexistence

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because emigrants from favorable habitats maintain populations in unfavorable habitats.

When examining the effects of habitat connectivity on both local (alpha) and regional (gamma) species diversity, most experimental studies have ignored the effects of heterogeneity in patch quality. For example, in an experimental investigation of arthropod communities inhabiting mosses with different degrees of fragmentation, Gilbert et al. (1998; see also Gonzalez et al. 1998) found that increasing connectance among identical local patches increased both local and regional measures of diversity. Similarly, Warren (1996), using protists in laboratory microcosms, showed that increasing rates of transfer between local communities (i.e., connectivity) tended to increase diversity within microcosms. However, habitat connectivity could have very different effects on local and regional diversity when there is considerable heterogeneity among habitat patches. Because regional diversity is the product of local diversity and the measure of inter-patch differences in species composition (also known as beta diversity [Whittaker 1972], see also Loreau 2000), increasing connectivity in systems containing high habitat heterogeneity can lead to the homogenization of patch communities (lower beta diversity) and consequently, lower regional diversity (Quinn and Harrison 1988, Harrison 1997, 1999, Amarasekare 2000, Mouquet and Loreau 2002).

In addition to the effects of habitat connectivity on local and regional patterns of species diversity, theory also predicts that the spatial arrangement (geometry) of patches could alter patterns of diversity. If adjacent patches are dissimilar in their local environment, species that favor certain habitat types should have a high probability of emigrating to different, potentially unfavorable types of habitat patches. These migrants from nearby patches (sources) can inflate local diversity by arriving in environments at the margins of their environmental tolerances (sinks) (Loreau and Mouquet 1999, Amarasekare and Nisbet 2001). However, given an environment with a high degree of autocorrelation (i.e., adjacent patches are similar), species that favor certain habitats would have a higher probability of emigrating to adjacent habitats of similar patch quality. In that case, we might expect most immigrants to a site to resemble those already present locally, and the connectivity of patches might have an overall weaker effect. Furthermore, both of these results vary with the dispersal abilities of the species within a regional pool (Travis and French 2000). Therefore, any geometric effects are likely coupled with the amount of connectivity between habitat patches.

In this paper, we present the results from a controlled experiment to examine the separate and interactive effects of connectivity rates and the spatial arrangement of heterogeneity on local and regional zooplankton diversity, as well as species compositional turnover

among localities (beta diversity). Specifically, using a diverse community of zooplankton in experimental aquatic mesocosms, we manipulated the amount of connectivity and the geometry of heterogeneous habitats within designated experimental regions. Our goal was to determine the effects of connectivity and habitat arrangement on species diversity at local and regional scales.

## Study system

Freshwater zooplankton represent an ideal ecological system to ask the questions posed above for a number of reasons: (1) zooplankton, including crustaceans (copepods and cladocerans) and rotifers, represent an important and diverse group of species throughout the world (Pennak 1989, Shurin et al. 2000); (2) their ecological interactions are known to constrain their local and regional biodiversity (Leibold 1999, Shurin 2000); (3) they frequently disperse among localities (vectored by animals and wind), and this dispersal is highly variable depending on the species and the juxtaposition of local water bodies (Maguire 1959, 1963, Jenkins and Buikema 1998, J. Shurin pers. comm.); (4) due to their short generation times, they respond rapidly to experimental treatments; (5) diverse communities are easily maintained in experimental mesocosms (Shurin 2001, M. Leibold pers. comm.); and (6) zooplankton community composition varies along environmental gradients, particularly the level of productivity (Leibold 1999, Dodson et al. 2000).

## Materials and methods

In this experiment, we created replicate zooplankton metacommunities, where each metacommunity, which we will call 'region', consisted of four local communities. Local communities were established in 70-l mesocosms (plastic containers commercially available as 'keg buckets'). In mid-July 1999, we filled each mesocosm three-quarters full with water (51 l). In each region, two mesocosms received no added nutrients (ambient concentrations were 2913 µg/l nitrogen; 4.5 µg/l phosphorus), to mimic oligotrophic conditions, while to the other two mesocosms, we added 180 µg/l of phosphorus (in the form of NaH<sub>2</sub>PO<sub>4</sub>) to mimic eutrophic conditions (we did not add nitrogen, because it was so high in abundance that it was not expected to be limiting to ecosystem productivity). In each mesocosm, we established diverse inocula of zooplankton and algae collected from a wide variety of freshwater habitats near the University of Pittsburgh's Pymatuning Laboratory of Ecology (Crawford County, PA [USA]). After 3 d, we repeated this inoculation to increase the probability

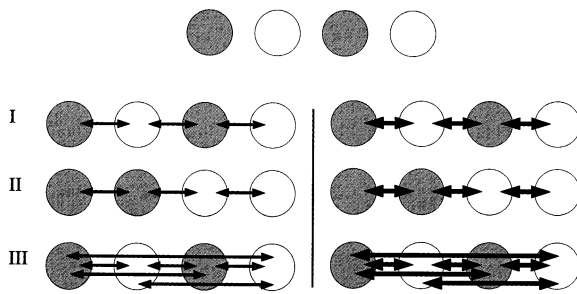


Fig. 1. Schematic representation of the seven experimental regions. Shaded circles represent eutrophic mesocosms (nutrients added), while unshaded circles represent oligotrophic mesocosms (no added nutrients). On the top row is the control region, with no connectivity among mesocosms. The four-mesocosm regions vary in the spatial arrangement of heterogeneity (the three rows designated I, II and III) and in connectivity rate (the larger arrow widths in the right-hand column represent increased connectivity). Note that while region II is positively spatially autocorrelated, other regions are not.

that species that could persist in these mesocosms had the opportunity to establish. In each mesocosm, we also introduced two small snails (*Physella gyrina*) to retard periphyton growth, and to recycle nutrients into the water column so that they would be available for plankton (Leibold and Wilbur 1992).

In order to test the importance of habitat geometry and connectivity, we manipulated the amount and arrangement of connectivity among mesocosms in the regions (Fig. 1). Two types of regions tested the importance of neighboring patch type on metacommunity composition. Type-I regions consisted of alternating oligotrophic and eutrophic mesocosms, and thus were negatively spatially autocorrelated in their patch arrangement. In type-II regions, by contrast, we placed the two oligotrophic and eutrophic mesocosms adjacent to each other, creating a positively spatially autocorrelated arrangement of habitat patches. In the final, type-III regions, we created a connection from each mesocosm to every other mesocosm, to examine the effect of increasing habitat connectivity on local and regional diversity apart from any geometric effects (Fig. 1). To compare the rates of habitat geometry versus the rates of habitat connectivity, we conducted this experi-

ment at two levels of local community connectivity. We further established a region type (consisting of four local communities) where there was no dispersal, to serve as the baseline for all array types (one of these regions was eliminated from our analysis, since a mesocosm within it cracked and drained during the experiment). Therefore, there were seven types (treatments) of four-mesocosm regions. Each region type, consisting of four mesocosms, was replicated four times for a total of 112 mesocosms.

We manipulated habitat connectivity by moving potential dispersal vectors (fuzzy tennis balls) among the mesocosms within a region (each with a 62-cm-long piece of twine hanging downwards into the mesocosms). Tennis balls were intended to mimic zooplankton passively dispersing among water bodies via animal (e.g., waterfowl or mammal) vectors. On average, each tennis ball ( $N = 12$ ) transferred from a mesocosm to a container of distilled water contained 3.3 species (19 individuals), indicating that the tennis balls were an effective passive dispersal agent (Table 1). To achieve different degrees of connectivity among local communities within regions, we moved tennis balls between mesocosms at three different rates; never, once every 5 d, and once every 10 d. In type-I and type-II regions, we placed one tennis ball in each of the outer-most mesocosms, and two in each of the inner mesocosms. After an hour, we lifted the tennis balls out of their 'donor' mesocosm, allowed them to drip dry for one minute, and then placed each tennis ball into a neighboring mesocosm. After a second hour, we removed the tennis balls, rinsed them with tap water, and allowed them to dry thoroughly before their next use. In type-III regions, where all mesocosms were equally connected to each other, we placed three tennis balls into each mesocosm. After an hour, we moved each ball to a different mesocosm in the region, such that each mesocosm exchanged a tennis ball with every other mesocosm in the region.

The experiment ran for 50 d, which is enough time for several generations of most of the zooplankton species used in this experiment. Further, several species were observed to go extinct, while others maintained relatively constant densities over much of the experiment (personal observation). Given the fast generation

Table 1. The effectiveness of tennis balls as passive zooplankton dispersers.

Species	Mean individuals dispersed	Percent of dispersed individuals (by mass)	Percentage of all mesocosms (by mass)
<i>Ceriodaphnia reticulata</i>	13.58	0.72	0.59
Ostracoda	2.00	0.01	0.01
<i>Diaicyclos thomasi</i>	0.92	0.14	0.06
Copepod nauplii	0.83	0.03	0.09
<i>Chydorus sphaericus</i>	0.67	0.09	0.21
<i>Euchlanis</i> spp.	0.58	0.00	0.00
<i>Mesocyclops edax</i>	0.42	0.01	0.02
All species	19.00		

Table 2. Univariate ANOVA results from the analysis comparing among treatments with varying rates of connectivity.

Source	SS	df	MS	F	P
Local richness	0.003	1,18	0.003	0.112	0.742
Regional richness	2.466	1,18	2.466	3.848	0.065
Percent similarity	0.525	1,18	0.525	8.830	0.008

times of most of the zooplankton species in these mesocosms, and their fecund nature, we expect that this time was long enough for most species to approach their steady state densities. Indeed, similar experiments have shown that zooplankton abundance and diversity changes considerably over the first 15–20 d, but then remains relatively unchanged (E. Bond and J. Chase unpubl.).

After 50 d, we sampled each of the mesocosms using a 5 cm diameter  $\times$  0.5 m PVC tube sampler that sampled on average, 0.51 of water. We took one sample from each mesocosm. We poured collected water through a 48- $\mu$ m mesh (allowing collection of all crustaceans and rotifers), and preserved it in acid Lugol's solution for later identification and enumeration. In each sample, we subsampled a known volume, and counted individuals under a dissecting microscope until either a minimum of 200 individuals was reached or until all individuals were counted. We identified each individual to species or, in some cases, genus. In each sample, we measured the lengths of the first 20 individuals of each species as a random sample to obtain biomass estimates. Lengths were converted to biomass using published length-weight regressions for cladocerans, and the length volume relations for rotifers (Dumont et al. 1975, McCauley 1984, Lawrence et al. 1987).

For each sample we performed rarefaction to obtain comparable measures of species richness among samples that varied in the numbers of individuals subsampled. For local richness values, we averaged rarefied richness values for all four mesocosms within a region, in order to account for the fact that replication took place at the regional level. We also calculated the percent similarity (PS) in species composition (Gauch 1982, Pielou 1984) among each of the local communities within the entire region. PS is an index of the similarity of local communities in relative species abundances (i.e., 0 represents completely different communities, while 1 represents identical communities). One minus PS is conceptually similar to beta-diversity, but is not similarly confounded due to differences in total regional diversity (Lande 1996). PS data were arcsine square root transformed before analysis. We calculated both richness and similarity indices based on species' estimated biomass rather than the number of individuals because of the large degree of variation among the average sizes of different zooplankton species.

We performed data analyses using MANOVA with the spatial arrangement of heterogeneity, rate, and rate  $\times$  geometry interactions as factors and average diversity of all mesocosms within a region, total regional diversity, and the percent similarity within the entire region as responses. Due to the unbalanced design of this experiment, we first ignored the unconnected arrays in our analysis, allowing for a fully factorial MANOVA comparing the effect of geometry, rate, and rate  $\times$  geometry. Next, to further examine the effects of the rate of connectivity apart from the geometric arrangement of heterogeneity, we performed ANOVAs using the subset of fully connected arrays (type-III regions) and the treatment in which mesocosms within regions were unconnected.

In addition to the diversity and similarity indices, we also analyzed the responses of all species to the treatments in MANOVA, followed by univariate ANOVAs to explore for species-specific responses to the manipulations of the spatial arrangement of heterogeneity and connectivity. All analyses were performed using SYSTAT 9.0.

## Results

Results from the factorial part of our experiment (connectivity rate  $\times$  geometric arrangement) showed that: (1) connectivity showed a significant effect (MANOVA: Wilks' lambda = 0.387;  $F = 8.442$ ;  $df = 3,16$ ;  $P = 0.001$ ), (2) the spatial arrangement of heterogeneity had no significant role in determining diversity or relatedness at any level (Wilks' lambda = 0.979;  $F = 0.056$ ;  $df = 6,32$ ;  $P = 0.999$ ), and (3) there was no geometry  $\times$  rate interaction (Wilks' lambda = 0.618;  $F = 1.450$ ;  $df = 6,32$ ;  $P = 0.227$ ).

We further explored the significant effect of connectivity rate by comparing both local and regional patterns in array type-III (eliminating the geometry effect), and adding the unconnected region treatment. Univariate responses of local richness, regional richness, and percent similarity (PS) are presented in Table 2. Specifically, we found no effect of connectivity rate on average local species richness (Fig. 2) (we also found no effects on local species richness when high nutrient and low nutrient mesocosms were analyzed separately). However, at the highest level of connectivity, regional species richness decreased (Fig. 3). Finally, we also found that with increased rates of connectivity, there was an

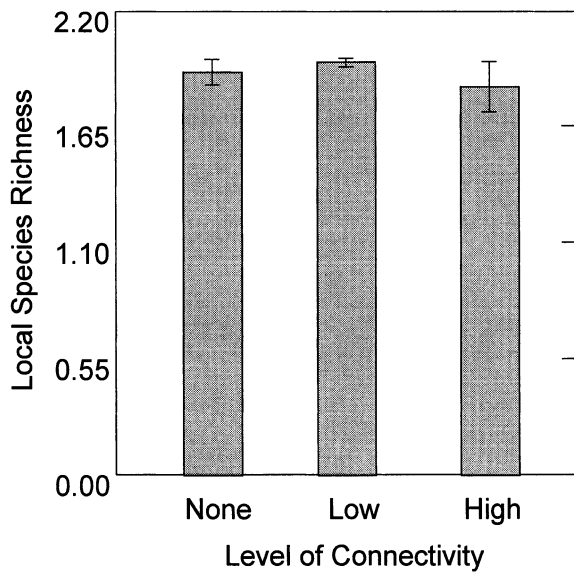


Fig. 2. Increased connectivity had no effect on local species richness. Data shown are from an analysis independent of the spatial arrangement of heterogeneity that included non-connected and completely connected arrays only. There were no significant differences among treatments at the local scale.

increased degree of species compositional relatedness (percent similarity) between mesocosms within an entire array (Fig. 4).

Because all of the community-level variables analyzed represent the distillation of a considerable amount of information on the species involved, we present representative results from two regions of mesocosms,

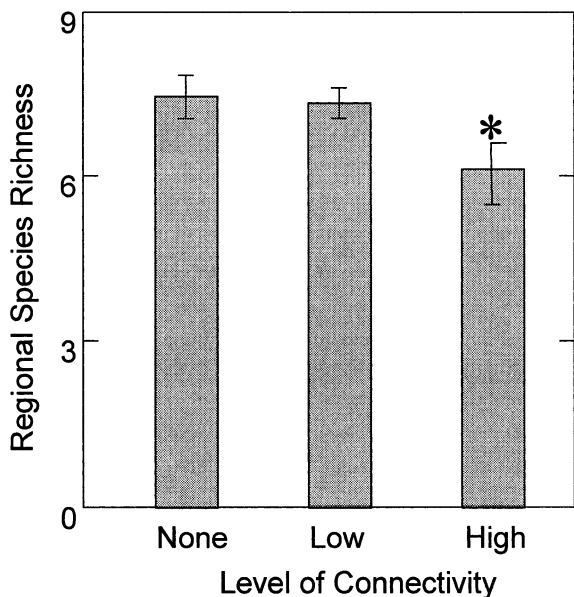


Fig. 3. Increased connectivity decreased regional species richness. Data shown are as in Fig. 2. Bars with an asterisk indicate a significant difference (Tukey's hsd;  $P < 0.06$ ).

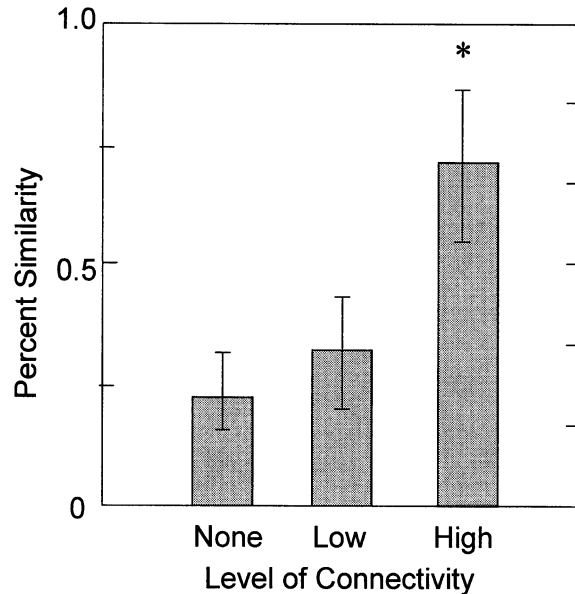


Fig. 4. Increased connectivity increased similarity. Data shown are as in Fig. 2. Asterisks are as in Fig. 3.

unconnected and highly connected, that showed significant differences in regional species richness in Table 3. Note that in this representative case, two species went extinct (*Mesocyclops edax* and *Keratella* spp.), and one nearly went extinct (*Euchlanis* spp.) in the connected regions, whereas all of these species were present in at least one mesocosm in the unconnected regions.

In addition to the effects of rates of connectivity on patterns of species diversity and similarity, we explored the individual responses of each species to the connectivity rate (but not geometry) treatments. Of all possible effects, we found that a relatively common zooplankter, *Ceriodaphnia reticulata*, exhibited significantly higher densities in highly connected regions (ANOVA;  $F = 5.327$ ;  $df\ 2,8$ ;  $P = 0.034$ ) (Fig. 5). This was largely the result of increased population densities; only 6 of 112 local *C. reticulata* populations went extinct.

## Discussion

Metapopulation theory predicts increasing species persistence with increasing rates of dispersal among patches (habitat connectivity), and has been supported in a variety of experimental systems (Hanski 1999). Further, to date, experimental studies of metacommunities have typically shown that increasing connectance among local communities increases diversity at the local and regional scales (Warren 1996, Gilbert et al. 1998, Gonzalez et al. 1998). We found a different response, but one that is consistent with a perspective from the emerging theory of metacommunities (Loreau and Mouquet 1999, Amarasekare 2000, Amarasekare and

Table 3. The biomass of each species within mesocosms from representative unconnected and highly connected regions. Low and high refer to the two mesocosms within each region with low or high nutrients, respectively. Numbers given for each species are estimates of biomass (see text).

Taxon	Species	Unconnected region				Connected region			
		Low	Low	High	High	Low	Low	High	High
Cladocera	<i>Ceriodaphnia reticulata</i>	4.39	0.00	78.94	81.41	4.39	0.18	12.32	24.49
	<i>Chydorus sphaericus</i>	49.06	4.06	31.85	21.59	8.34	0.26	0	1.44
	<i>Daphnia pulex</i>	0	36.05	0	0	0	0	0	29.43
Copepoda	<i>Diaacyclops thomasi</i>	0	0	7.82	0	3.49	46.5	11.99	0
	<i>Mesocyclops edax</i>	0.69	4.1	0	0	0	0	0	0
Rotifera	<i>Euchlanis</i> spp.	0.13	0	0	0	0	<0.001	0	0
	<i>Nothalca</i> spp.	0	0	0.01	0	0.29	0.01	0.001	0
	<i>Keratella</i> spp.	0	0	0	0.04	0	0	0	0
Ostracoda	Unidentified	2	15.54	88.88	59.31	13.63	2	6	8

Nisbet 2001, Klausmeier 2001, Mouquet and Loreau 2002).

Despite our expectations that variation in the geometric arrangement of habitat patches would alter community structure, we found no main or interactive effects of habitat geometry on local and regional diversity, or on the dissimilarity of local habitats. One reason why we might have found no effect of habitat arrangement on zooplankton community structure would be if the differences in nutrient conditions were so great that certain species from one nutrient treatment simply could not survive in the other. This was not the case with the most common zooplankton species, which seemed to be able to maintain positive population growth in both habitat types. However, the rarer species (e.g., many of the rotifers), which drive the patterns of species diversity, may be more sensitive to environmental conditions. Unfortunately, we are unable to discern whether this was the case statistically, since most of the rarer species were quite heterogeneous in their distribution both within and among treatments.

A second related reason why we might not have found an effect of the habitat arrangement on local or regional community attributes would be if these zooplankton communities were unlikely to exhibit the sorts of source-sink dynamics that would be necessary to observe such an effect (Loreau and Mouquet 1999, Amarasekare and Nisbet 2001). Perhaps because these zooplankton species have such rapid generation times, they are able to persist in habitats where they have positive population growth, but quickly go extinct in habitats where they have negative growth, and are not able to persist in sink habitats long enough to be rescued by immigrants from sources.

Thus, although we did not find any significant effects of the geometric habitat arrangement on local or regional community attributes, we do not intend this discussion to imply that they do not, or are unlikely to, exist in other systems. Specifically, we might expect that in systems where source-sink effects are likely to persist on time scales on the same order as immigration rates,

the arrangement of heterogeneous habitats might have more significant effects.

In contrast to the effects of geometric habitat arrangement, we did find an effect of the rate of habitat connectivity on community structure. Specifically, when we experimentally increased the connectance among local communities, we found that while there was no effect on local species diversity (Fig. 2), there was an overall decrease in the diversity of species within regions of connected experimental communities (Fig. 3). Further, we found that the percent similarity (PS) of species composition among communities within an experimental region increased with increasing connectance (Fig. 4). That is, as the degree of connectance among regions increased, communities within regions became more similar to one another, and thus while there was no effect of connectance on local species diversity, species diversity within the entire region declined. Although we do not have the statistical power to

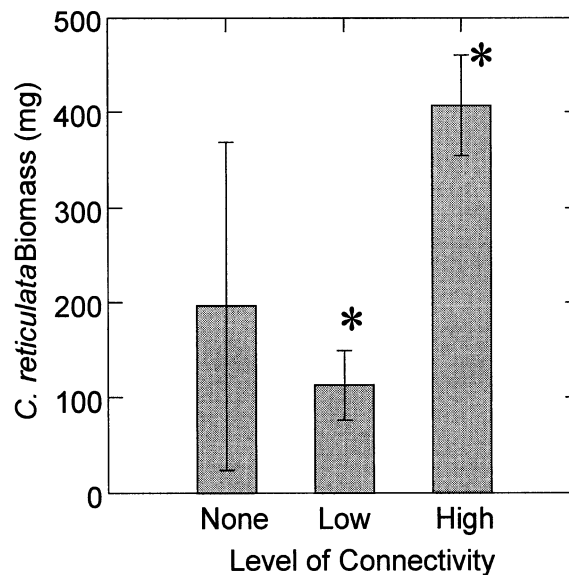


Fig. 5. Increased connectivity increased the abundance of *Ceriodaphnia reticulata*. Data and asterisks are as in Figs 3, 4.

fully evaluate the causes of this result, we suggest that these results primarily occurred because connectance, by increasing the propensity of common species to establish in all mesocosms, caused the rarer species to go extinct. Indeed, a visual analysis of the representative data in Table 3 shows this to be the case, where the species that could not persist when communities were connected, were quite rare, and only persisted in one or two mesocosms when communities were not connected.

As has been suggested from empirical surveys of connected and unconnected habitats (Harrison 1997, 1999, Quinn and Harrison 1988), as well as theoretical modeling (Hastings and Gavrilets 1999, Amarasekare 2000, Mouquet and Loreau 2002), increased connectance among local communities can lead to lower overall species diversity. We suggest that this result will be particularly prominent when isolated communities diverge in community composition, either as a result of environmental or historical factors. We further suggest that previous experimental studies of meta-community structure may have found positive effects of connectivity on regional diversity (e.g., Warren 1996, Gonzalez et al. 1998, Gilbert et al. 1998) because environmental conditions among localities were intentionally quite homogeneous.

To fully explore why we found decreased regional species diversity with increased habitat connectance, we refer to the dynamics of one of the dominant species among all of our experimental mesocosms, and the one species that showed significant responses to the imposed treatments, *Ceriodaphnia reticulata*. This species is a widespread littoral species, with a strong preference for shallow, eutrophic habitats (Desmarais and Tessier 1999). However, larger species often out-compete *C. reticulata* in deeper, oligotrophic waters (Gliwicz and Lampert 1993). Since *C. reticulata* naturally fares well in eutrophic environments, we might not expect increased connectivity to drastically alter its effect upon eutrophic communities, since it should be favored there regardless of regional connectivity. However, in this species' less favored habitat, oligotrophic environments, we might expect that increased connectivity could offer *C. reticulata* increased opportunity to establish higher population densities.

In our experiment, we observed a strong response by *C. reticulata* to our dispersal treatment (it frequently adhered to the tennis balls); we note, however, that the portion of dispersers that were *C. reticulata* was similar to the species' overall density in mesocosms (and thus, it did not necessarily have a disproportionate propensity for dispersal). Furthermore, although this species rarely went extinct in these mesocosms (6 of 112), increasing connectance allowed it to achieve considerably higher densities within individual mesocosms (Fig. 5), and in particular, the olig-

otrophic mesocosms. Finally, we found that the density of this species was much more variable in mesocosms with no connectance (see Fig. 5). This suggests that the density to which *C. reticulata* achieved in a mesocosm was at least in part stochastic. Thus, in unconnected mesocosms, this species sometimes achieved very high densities in all mesocosms, and other times was quite rare. However, in connected mesocosms, possibly because of repeated invasions through dispersal, this species was able to achieve consistently higher densities in all mesocosm types.

We suggest that the increased density of *C. reticulata* at high rates of connectivity may, in part, explain the increase in percent similarity (PS) among local communities within a region (i.e., decreasing  $\beta$ -diversity). Furthermore, because regional ( $\gamma$ ) diversity is the product of ( $\beta$ - and  $\alpha$ -diversity (Whittaker 1972; also see Lande's 1996 discussion of additive partitioning of diversity), any mechanism that decreases  $\beta$ -diversity without significantly altering  $\alpha$ -diversity will lead to a decrease in regional diversity, as we observed in this study. Thus, it is possible that *C. reticulata*, by virtue of dominating both habitat types with high connectivity, was able to preclude the invasion (or enhance the extinction) of rarer species, increase the species compositional similarity among mesocosms, and lead to a decrease in overall regional species diversity. Indeed, this is exactly what happened in the representative mesocosm regions shown in Table 3. Of course, given the coarse nature within which we collected our data, and the fact that our experiment was not designed to test for mechanisms of the responses, these will remain speculations until further study.

Finally, although not explicitly designed as such, our work also points to a critical issue in conservation ecology. Habitat corridors (i.e., connections among otherwise isolated habitats) are often discussed as an important conservation tool for the preservation of individual species as well as overall diversity. Indeed, this was one of the main conclusions of the metacommunity study by Gilbert et al. 1998 (see also Gonzalez et al. 1998). However, our study suggests that while habitat corridors may increase local and regional diversity when habitat fragments are relatively homogeneous (as they were in Gilbert et al. 1998), they may actually decrease regional diversity when there is heterogeneity among habitat fragments (see also Quinn and Harrison 1988, Harrison and Bruna 1999).

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