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The effects of habitat connectivity and regional heterogeneity on artificial pond metacommunities

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Abstract Habitat connectivity and regional heterogeneity represent two factors likely to affect biodiversity across different spatial scales. We performed a 3×2 factorial design experiment to investigate the effects of connectivity, heterogeneity, and their interaction on artificial pond communities of freshwater invertebrates at the local (α), among-community (β), and regional (γ) scales. Despite expectations that the effects of connectivity would depend on levels of regional heterogeneity, no significant interactions were found for any diversity index investigated at any spatial scale. While observed responses of biodiversity to connectivity and heterogeneity depended to some extent on the diversity index and spatial partitioning formula used, the general pattern shows that these factors largely act at the β scale, as opposed to the α or γ scales. We conclude that the major role of connectivity in aquatic invertebrate communities is to act as a homogenizing force with relatively little effect on diversity at the α or γ levels. Conversely, heterogeneity acts as a force maintaining differences between communities.

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Introduction

Understanding the processes that control biodiversity has proven to be one of community ecology's most challenging problems (Hutchinson 1961; Clark et al. 2007), and also one attracting considerable interest given the present high rates of biodiversity loss (Pimm et al. 1995; Thomas et al. 2004; Worm et al. 2006) and the relationship between biodiversity and ecosystem functioning, especially during times of disturbance (Loreau et al. 2001).

Many of the recent theoretical developments concerning the concept of biodiversity have involved the idea that ecological communities, while discrete, may be linked into larger aggregates by dispersal, creating so-called metacommunities (Leibold et al. 2004). One of the major conclusions emerging from metacommunity theory has been that biodiversity is affected not only by local processes, such as competition and predation, but also by regional factors, such as habitat connectivity and regional heterogeneity (Leibold et al. 2004). As a result, the relationship between habitat connectivity and local (α), among-community (β), and regional (γ) diversity has recently received much attention both empirically and theoretically. Despite this attention, few reliable general statements can be made about how regional factors affect biodiversity. Theoretically, there is reason to expect that α diversity has a unimodal positive relationship with connectivity, β diversity a monotonic negative relationship, and γ diversity a 'humped' monotonic negative relationship (Mouquet and Loreau 2003); however, these predictions are not always born out

by empirical studies. While most empirical studies find that dispersal increases α richness (Cadotte 2006a; Davies et al. 2009; but see Shurin 2000; Forbes and Chase 2002), the exact nature of this relationship is unclear, with some studies finding a monotonic positive response of richness to increasing connectivity (Gilbert et al. 1998; Warren 1996a) and others finding a unimodal response (Kneitel and Miller 2003; Cadotte 2006b). The relationship between β diversity and connectivity has proven empirically more consistent, typically demonstrating a monotonic decrease with increasing connectivity (e.g., Warren 1996b), but even this is not invariable (Cadotte 2006b). Finally, the effects of connectivity on γ richness have proven to be quite variable, with a number of empirical studies finding no effect (Warren 1996a, b; Cadotte 2006b; Cadotte et al. 2006; Davies et al. 2009), increases with connectivity (Kneitel and Miller 2003), or decreases with connectivity (Forbes and Chase 2002; Cadotte and Fukami 2005; Cadotte 2006b).

Surprisingly, despite the importance of regional heterogeneity to many models of competition and predation, relatively few experimental studies have attempted to explicitly investigate the interaction between habitat connectivity and regional heterogeneity on biodiversity (but see Cadotte 2006b; Davies et al. 2009). As one of the primary differences between metacommunity perspectives is the amount of regional heterogeneity assumed (Leibold et al. 2004), the presence or absence of heterogeneity should determine which mechanisms contribute to determining biodiversity. For example, while some mechanisms of competitive coexistence in metacommunities, such as the competition-colonization trade-off, do not require regional heterogeneity to operate (Hastings 1980), other mechanisms do, such as regional niche differentiation and mass effects (Mouquet et al. 2005). Consequently, it is likely that regional heterogeneity will play a strong role in determining the response of biodiversity to connectivity, and it is possible that such an interaction has contributed to previously observed differences in the relationship between connectivity and species richness (Forbes and Chase 2002).

Here we present the results of an artificial pond experiment designed to investigate the potential interaction between habitat connectivity and regional heterogeneity on biodiversity of communities of freshwater invertebrates over a variety of spatial scales. While most metacommunity experiments to date have focused on species richness, no doubt due to its intuitive meaning, we extended our analyses to Simpson diversity (Simpson 1949) and a measure of functional diversity (FD) (Petchey and Gaston 2002) to evaluate how different aspects of biodiversity respond to regional processes. While each measure is informative, the impact of metacommunity processes on some ecosystem properties may be better evaluated with the latter two as Simpson diversity takes relative species abundances into account, and there is some evidence that measures of functional diversity correlate more strongly with ecosystem properties than do measures of species richness (Tilman et al. 1997; Barnett and Beisner 2007).

Methods

Experimental design

To test whether the effects of connectivity on biodiversity depended on regional heterogeneity we conducted an artificial pond mesocosm experiment at the Queen's University Biological Station in the summer of 2007. In total, seventy-two 350-L ponds were set up, grouped into 18 regions of four ponds each. The experiment had a 3×2 factorial design with three levels of habitat connectivity (none, low, and high), and two levels of regional heterogeneity (homogeneous regions, heterogeneous regions) (Online Resource A). Each cell of the design contained three replicate regions.

Connectivity levels were defined by transferring set volumes of water (and any included organisms) between ponds within a region on a weekly basis. In regions with no connectivity, mock transfer events were performed by transferring samples of water back to the pond from which they originated; in regions with low connectivity, 3 L of water was transferred from each pond to every other pond within the region (total turnover per pond per week 9 L); in regions with high connectivity, 12 L of water was transferred (total turnover per pond per week 36 L). While our high dispersal treatment is relatively strong, our goal was to elicit strong responses to connectivity to ensure that the response of an extremely well mixed region would be observed. Prior to all dispersal events the ponds were gently homogenized with a paddle, and the necessary volume of water was transferred by tube sampler.

Heterogeneity was modified using pond substrate. Homogeneous metacommunities were composed of four ponds with identical substrate (bare tank with no added substrate), and heterogeneous metacommunities were composed of four ponds, each with a different substrate (bare tank, rock substrate, short artificial-macrophyte substrate, long artificial-macrophyte substrate). The same substrate combinations were present in each replicate. We chose substrate as the basis for our heterogeneity treatment as substrate has previously been shown to have effects on zooplankton community composition (Declerck et al. 2007), and we felt it would support clear niche differentiation among littoral communities.

The ponds were created in 378-L cattle tanks filled with 350 L of lake water filtered through a 50-μm mesh. Exogenous colonization during the experiment was minimized

by covering the ponds with a 1-mm mesh and placing them in a sheltered field 130 m from the nearest water body. Despite these precautions, over the course of the experiment some ponds were colonized by water mites and *Chaoborus*, and as such these taxa are included in biodiversity results. Treatments were randomly assigned to metacommunities throughout the field, and substrates were randomly assigned to tanks within metacommunities. Each pond was inoculated with a homogenized mixture of aquatic invertebrates collected from ten lakes close to the Queen's University Biological Station (Online Resource B) by pelagic hauls and littoral sweeps with nets of 50-μm mesh. Such use of invertebrates collected from distinctly different habitats creates a hyperdiverse inoculum which ensures that the initial biota will be diverse enough to respond to the selection gradients imposed by treatments; it also helps ensure that results are not simply idiosyncratic responses of a particular community to the treatments (Declerck et al. 2007). Before seeding the ponds, we inspected the collected samples and manually removed macroinvertebrates.

The ponds were inoculated on June 3, 2007 with 1-L colonist aliquots dispensed from a constantly mixed tub to provide nearly identical initial communities at roughly ambient densities. The experiment ran 12 weeks, and ponds received nutrient additions (0.3914 g $NaNO_3$ and 0.01 g NaH_2PO_4) at 2-week intervals until July 13, and every 3 weeks thereafter. The ponds were sampled on August 27 by gently homogenizing the tanks and then capturing 6 L of water by tube sampler. The samples were filtered using a 50-μm mesh, and organisms were anesthetized with club soda and preserved in 5.5% buffered sugar formalin.

Invertebrate enumeration and identification

A sample from each pond representing an unconcentrated volume of 0.9 L (total pond volume 0.257%) was counted in six successive subsamples. This level of sampling effort was determined by constructing subsample-based taxon accumulation curves for the first four ponds counted and terminating subsampling past a level where richness appeared to plateau. This level of sampling effort also generated richness asymptotes in the ponds with the greatest abundance, least abundance, and greatest richness (Online Resource C), indicating that while our data were not rarified, raw richness data are likely indicative of actual trends in richness, and not simply of variation in richness due to variation in abundance (Gotelli and Colwell 2001).

Each subsample was investigated at 40× magnification and, when necessary, specimens were dissected and identified at 100–400× magnification. Monogonont rotifers were identified to genus, and bdelloid rotifers were identified to class Bdelloidea. Cladocerans and adult copepods were identified to species, with the exception of individuals of *Bosmina* and *Ceriodaphnia*, which were lumped together at the genus level. Immature copepods were either identified to order (copepodids) or simply to class (nauplii) and, as such, were excluded from the biodiversity analyses. Chaoborids, cnidarians, gastrotrichs, water mites, and turbellarians were identified to genus; ostracods and tardigrades were identified simply to Ostracoda and Tardigrada. All of these taxa were included in all analyses. The very few individuals that could not be identified to the desired taxonomic resolution were discarded.

Data analysis

To determine how our treatments affected different aspects of diversity, we analyzed three different biodiversity indices, all of which address different aspects of diversity: (1) richness, the raw number of species present; (2) Simpson diversity (Simpson 1949; Lande 1996), which is a measure that considers both richness and relative abundances, which we in turn converted to its 'numbers equivalent' (the number of equally common elements that produces the given value of the diversity index) following Jost (2006, 2007); (3) FD (Petchey and Gaston 2002), which is an index of functional diversity. Recently, there has been some controversy about how biodiversity should be spatially partitioned (Ricotta 2010), with some authors arguing for an additive relationship between mean α, γ, and β diversity (Lande 1996), while others have favored multiplicative methods for deriving β diversity (Whittaker 1972; Jost 2007). Consequently, we employed additive formulae for partitioning richness and FD (Lande 1996; Ricotta 2005), and multiplicative formulae for partitioning β richness (to allow comparison with additive partitioning) and Simpson diversity (Jost 2007). No multiplicative partition was used for β FD, for which no specific formula is available, and no additive partition was employed for Simpson diversity due to the lack of independence between α and β diversity with this metric when partitioned additively (Jost 2007). While we acknowledge that two methods of partitioning open the door to the possibility that patterns differ for reasons of analysis, because we partition richness both ways, it represents a form of diversity against which both Simpson diversity and FD can be compared.

FD was calculated using the method of Petchey and Gaston (2002) with the following species traits: habitat type (also used to evaluate the hypothesis that trends in treatment effects on richness would differ between littoral and pelagic communities), trophic level, feeding method, and body length (Online Resource D). These traits were also used by Barnett et al. (2007) to calculate the FD of zooplankton communities due to their greater reliability than other life-history parameters, as the latter may be strongly affected by environmental conditions; our assignment of traits generally

follows their classificatory scheme to provide compatibility with their study. The first three traits were assigned to species based on data reported in the published literature or personal observation, although it was occasionally necessary to generalize traits from closely related species or from a different trait (e.g., mastax morphology in rotifers was used to infer feeding method). Lengths represent experiment-wide averages of measurements taken during counting (the first 10 individuals of each taxon encountered in each pond were measured to the nearest 25 μm, although due to a change in protocol, measurements for rotifers were only available for 48 ponds), except for the three species in which measurements were not available and data were obtained from the literature. Categorical traits were ranked before conversion to a standardized Euclidean distance matrix, which was used to build a dendrogram by the unweighted pair-group average method. The dendrogram was built for the experiment-wide contingent of species. α and γ FDs were calculated as the sum of branch lengths for all species present in the focal pond or region, respectively. This all-species-dendrogram approach guarantees that FD is set-monotonic and, therefore, that an additive framework is appropriate for spatial diversity partitioning (Ricotta 2005).

Two-way analysis of variance (ANOVA) was employed to investigate the effects of connectivity and heterogeneity on mean α, β, and γ biodiversity (all biodiversity indices), with Tukey's Honestly Significant Difference (Tukey HSD) tests being employed for post hoc analysis where appropriate. Assumptions of all statistical tests were checked visually. As ANOVA is robust to violations of normality and heteroskedasticity of variances when the design is balanced (Zar 1999), violations of these assumptions should have had little effect on our results. Transformations were performed on data when they clearly improved normality or homogeneity of variances (Simpson data). All data analysis was performed in R ver. 2.7.0 (R Development Core Team 2008) using the packages car (ver. 1.28), cluster (ver. 1.11.11), stats (2.7.0), and vegan (ver. 1.13-1).

Results

Both habitat connectivity and regional heterogeneity had effects on biodiversity, although the nature of these effects depended on the form of biodiversity analyzed. Connectivity had a significant positive effect on mean α richness ($P = 0.038$), but no significant effect on mean α Simpson diversity, nor on mean α FD (Fig. 1, Table 1). At the γ scale, no treatment had significant effects on any

Fig. 1 Aquatic invertebrate diversity at mean local (α) and regional (γ) scales [mean ± standard error (SE)] for homogenous (*white bars*) and heterogenous (*grey bars*) regions with three levels of connectivity: **a**, **b** species richness, **c**, **d** Simpson diversity, **e**, **f** functional diversity index (*FD*). *Uppercase letters above bars* indicate significant differences ($P < 0.05$) between connectivity levels based on Tukey HSD tests. There were no significant differences in heterogeneity
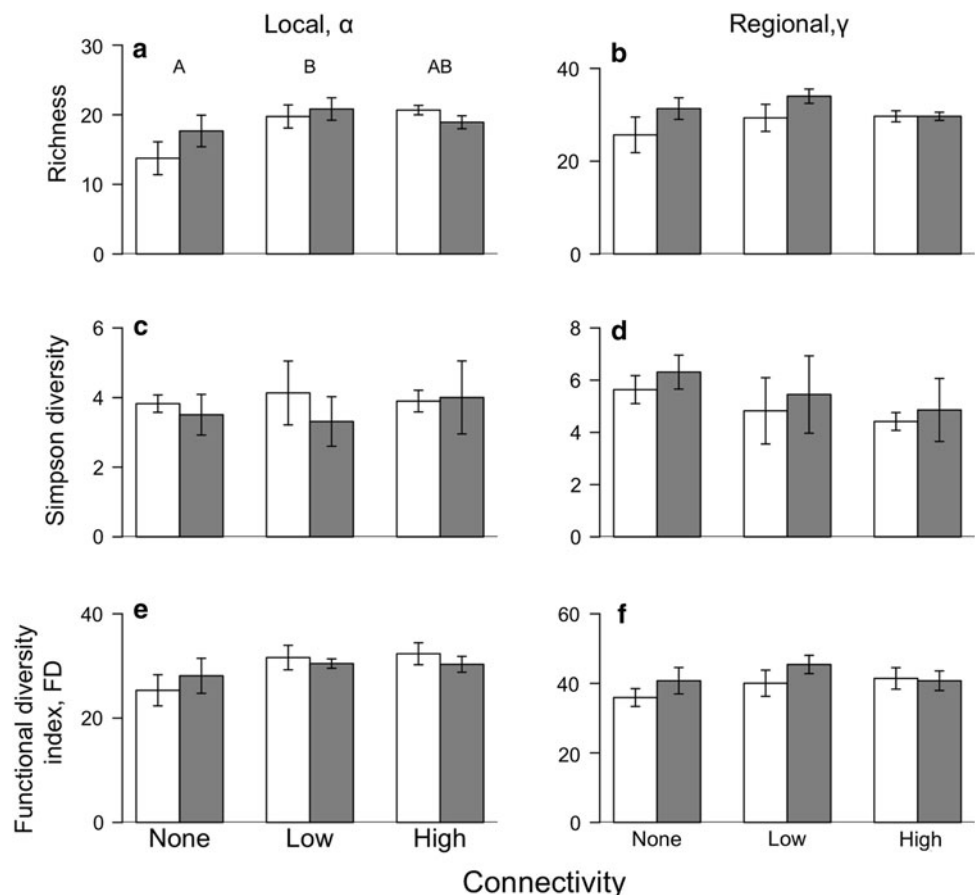
Table 1 Analyses of variance of mean α and γ richness, log Simpson diversity, and functional diversity by connectivity, heterogeneity, and their interaction

| Biodiversity factor	α Richness			γ Richness		
	df	F	P	df	F	P
Connectivity	2	4.36	0.038**	2	0.93	0.422
Heterogeneity	1	0.61	0.451	1	3.21	0.098*
Connectivity × heterogeneity	2	1.38	0.288	2	0.83	0.461
Error	12			12		
	α Simpson diversity			γ Simpson diversity		
	df	F	P	df	F	P
Connectivity	2	0.09	0.910	2	1.05	0.380
Heterogeneity	1	0.69	0.422	1	0.24	0.630
Connectivity × heterogeneity	2	0.14	0.872	2	0.02	0.977
Error	12			12		
	α FD			γ FD		
	df	F	P	df	F	P
Connectivity	2	2.39	0.134	2	0.99	0.400
Heterogeneity	1	0.00	0.948	1	1.54	0.239
Connectivity × heterogeneity	2	0.59	0.570	2	0.57	0.582
Error	12			12		

α Local level, γ regional level, FD functional diversity

* $0.05 < P < 0.10$,
** $P < 0.05$

biodiversity index, although there was a trend towards higher γ richness in heterogeneous ponds ($P = 0.098$) (Fig. 1, Table 1). The majority of effects of connectivity and heterogeneity manifested at the β scale (Fig. 2, Table 2), where connectivity significantly lowered multiplicative β richness ($P = 0.001$) and β Simpson diversity ($P = 0.023$), as well as nearly significantly lowering additive β richness ($P = 0.061$). Conversely, heterogeneity significantly raised β Simpson diversity ($P = 0.034$) and additive β richness ($P = 0.021$), but not multiplicative β richness. Furthermore, heterogeneity nearly significantly raised β FD ($P = 0.061$). The effects of heterogeneity on β and γ richness appear to be independent of any one substrate type, as substrate type had no significant effect on the α richness of ponds from unconnected heterogeneous regions ($F_{3,8} = 0.10$, $P = 0.956$). Finally, the effects of connectivity and heterogeneity on richness depended on the habitat preference of species. When species were split into littoral and pelagic communities, the littoral community additive β richness was significantly affected by heterogeneity, but not connectivity, whereas pelagic community additive β richness was significantly affected by connectivity but not heterogeneity (Online Resource E).

Discussion

Environmental heterogeneity is one of the most important factors for maintaining biodiversity, an effect that has been demonstrated both theoretically and in zooplankton
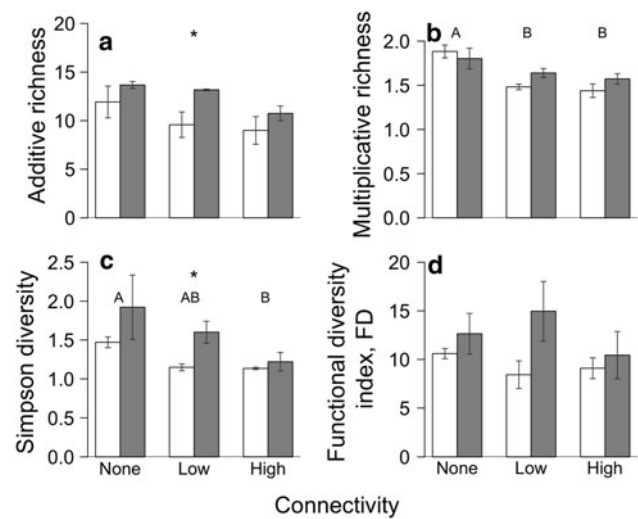
Fig. 2 Aquatic invertebrate diversity at the among-community (β) scale (mean ± SE) for homogenous (*white bars*) and heterogenous (*grey bars*) regions with three connectivity levels: **a** additive richness, **b** multiplicative richness, **c** Simpson diversity, **d** FD. *Uppercase letters above bars* indicate significant differences ($P < 0.05$) between connectivity levels based on Tukey HSD tests. *Asterisks* indicate a significant effect of heterogeneity ($P < 0.05$). Note that while untransformed Simpson diversity data are plotted, significance indications are based on transformed data

communities (Chesson 2000; Leibold et al. 2004). Indeed, heterogeneity in competitive conditions has been proposed as one of the key solutions to the paradox of the plankton (Hutchinson 1961) in that it allows different species to capitalize on different environmental conditions and

Table 2 Analyses of variance of β richness (additive and multiplicative), log Simpson diversity, and FD by connectivity, heterogeneity and their interaction

Biodiversity factor	β Richness (additive)			β Richness (multiplicative)		
	df	F	P	df	F	P
Connectivity	2	3.57	0.061*	2	12.30	0.001**
Heterogeneity	1	7.01	0.021**	1	1.39	0.261
Connectivity × heterogeneity	2	0.47	0.636	2	1.62	0.238
Error	12			12		
	β FD			β Simpson diversity		
	df	F	P	df	F	P
Connectivity	2	0.62	0.553	2	5.29	0.023**
Heterogeneity	1	4.28	0.061*	1	5.74	0.034**
Connectivity × heterogeneity	2	1.03	0.387	2	0.79	0.475
Error	12			12		

* $0.05 < P < 0.10$,
** $P < 0.05$

coexist across either space or time (Chesson 2000). As connectivity levels alter the extent to which species experience the range of environmental conditions available and modify the extent to which habitat patches are truly discrete, we expected that heterogeneity and connectivity would interact strongly in their effects on biodiversity. Yet despite significant effects of both connectivity and heterogeneity on biodiversity, we found no significant interaction between the two factors at any scale of biodiversity.

It is impossible to say conclusively why we did not observe an interaction, although many possible explanations do exist. While we examined a time scale that included many generations for most of the species involved, and roughly approximated seasonal dynamics important for zooplankton (Wetzel 2001), especially in small water bodies that may be temporary (Cáceres and Tessier 2004), we only analyzed samples for our communities at one time period. As biodiversity often responds dynamically to treatments, it is always possible that an interaction might have manifested over shorter or longer time scales. It is also possible that an interaction would not be observed if different processes operated to similar ends in homogeneous and heterogeneous metacommunities. For example, rescue effects and recolonizations might minimize stochastic local extinctions in homogeneous metacommunities, but local extinctions may also be minimized by dispersal in heterogeneous metacommunities, due to rescue effects and also mass effects maintaining species in sink habitats (e.g., Mouquet and Loreau 2003). Interestingly, while some previous microcosm experiments with protozoans have shown strong interactions between heterogeneity and connectivity (Cadotte 2006b), others have not found an interaction between the two (Davies et al. 2009), suggesting that interactions between connectivity and heterogeneity may not be a completely general phenomenon. Our experiment offers perhaps the first look at this problem

predominantly using zooplankton as the community under investigation, and it will be interesting to see if other studies investigating the same question with zooplankton find similar results.

Contrasting with the lack of significant interactions, significant effects of both connectivity and heterogeneity were observed independently of one another, largely at the β scale. Connectivity had a strong tendency to reduce β diversity, either significantly or nearly significantly, for species richness (both additive and multiplicative) and Simpson diversity, underlining the general ability for dispersal to homogenize the ponds within a metacommunity both when considering only species numbers (richness measures) and when considering relative abundances (Simpson diversity). Conversely, heterogeneity significantly or nearly significantly raised β diversity (with the exception of multiplicative β richness), suggesting that our substrate treatments were having the expected effect on the zooplankton community. It is worth noting that the different responses of additive and multiplicative β richness to heterogeneity are surprising. While they have different meanings, with additive representing the regional number of species not present in the local community and multiplicative representing the number of unique communities (Jost 2007), they both represent differences between communities within a region and, as such, they would be expected to increase with substrate heterogeneity. While this expectation is fulfilled on average in metacommunities with connectivity, in the no-connectivity treatment it is rather homogeneous regions that have higher multiplicative β richness (Fig. 2). Interestingly, β Simpson diversity, which also yields the number of unique communities, more resembles the patterns from additive β richness, which reinforces our suggestion that multiple biodiversity metrics incorporating different information may be necessary to successfully elucidate diversity patterns.

That the major effects of connectivity and heterogeneity are observed at the β scale is reasonable, given that the scale of treatments is between communities within a region, but connectivity and heterogeneity had effects also at the α and γ scales. Connectivity significantly affected α richness, with an average increase of approximately 4.6 species between no-connectivity and low-connectivity regions, but it did not raise Simpson diversity, implying that the additional species remained relatively rare in the ponds where they were maintained. Our data do not show the unimodal response of α richness to connectivity that is occasionally observed, which is surprising given the strong connectivity treatments we employed, suggesting that predictions of unimodal richness responses to dispersal may invoke connectivity levels that are unlikely to be often achieved in nature. Finally, at the γ scale there was a trend for higher γ richness in heterogeneous regions, suggesting that the greater β richness observed in these metacommunities translated to greater overall richness. Interestingly, while there was a trend towards higher β-FD with heterogeneity, connectivity had no significant effects on FD at any scale, implying that the increases in α richness and the losses of β diversity due to connectivity largely consisted of functionally redundant species. Of course, our ponds had relatively high initial diversity, and connectivity may have a stronger effect on both richness and functional diversity in systems that are depauperate in richness, such as habitats disturbed by acidification (Derry and Arnott 2007) or introduced species (Strecker and Arnott 2010).

Finally, it is worth considering that while our metacommunities were designed to resemble ecological conditions experienced by lentic invertebrate communities (especially those in small water bodies where fish are likely to be absent), natural communities would likely differ in initial community composition and undergo a process of community assembly quite different from the way in which our communities were formed, though our simultaneous introduction of many species may resemble rapid recolonizations of temporary ponds from egg banks (Cáceres and Tessier 2004). An additional caveat is worthy of mention: while we did not replicate heterogeneity per se, but instead replicated a homogeneous region and a heterogeneous region, we believe our results are generalizable outside of our particular substrate treatments. Supporting this assertion is the lack of an effect of substrate on local richness, which contrasts with the significant effect of heterogeneity on β diversity and suggests that our treatment ultimately created biotic heterogeneity, as intended. Consequently, we believe our results contribute strongly to research on how heterogeneity affects biodiversity. That being said, it is worth noting that when we subdivided our community into pelagic and littoral components, only the littoral community showed an effect of heterogeneity,

suggesting that environmental heterogeneity is always a function of the specific organismal response to a varying environmental component.

In conclusion, our experiment has investigated the effects of connectivity and heterogeneity on metacommunities of freshwater invertebrates. The results clearly demonstrate important roles for both regional heterogeneity and habitat connectivity in terms of affecting biodiversity, particularly at the β scale, thereby confirming the essential role of both factors in metacommunity ecology. Our results further suggest that, at least over seasonal time scales, biodiversity at the γ scale is primarily controlled by heterogeneity, whereas that at the α scale is primarily controlled by connectivity; however, these effects at the α and γ scales do not manifest when relative abundances and functional difference are considered and, therefore, may only be of marginal importance. Finally, while we predicted that a strong interaction between connectivity and heterogeneity would manifest itself in our metacommunities, no such interaction was observed, suggesting that other factors may underlie the varying observations of the relationship between habitat connectivity and biodiversity.

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