

METACOMMUNITY INFLUENCES ON COMMUNITY RICHNESS AT MULTIPLE SPATIAL SCALES: A MICROCOSM EXPERIMENT

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Abstract. Large-scale processes are known to be important for patterns of species richness, yet the ways in which local and larger scale processes interact is not clear. I used metacommunities consisting of five interconnected microbial aquatic communities to examine the manner in which processes at different scales affect local and metacommunity richness. Specifically, I manipulated the potential dispersal rate, whether dispersal was localized or global, and variation in initial community composition. A repeated-measures ANOVA showed that a low dispersal rate and intermediate distance dispersal enhanced local richness. Initial assembly variation had no effect on local richness, while a lack of dispersal or global dispersal reduced local richness. At the metacommunity scale, richness was enhanced throughout the time course of the experiment by initial compositional variation and was reduced by high or global dispersal. The effects of dispersal were contingent on the presence of initial compositional variation. The treatments also affected individual species occupancy patterns, with some benefiting from large-scale processes and others being adversely impacted. These results indicate that the effects of dispersal on species richness have a complex relationship with scale and are not solely divisible into “regional” vs. “local” scales. Finally, predictions of the manner in which dispersal rate structures communities appear dependent upon species compositional variation among communities.

Key words: *community assembly; dispersal; metacommunity; migration; regional effects; spatial scale; species diversity; temporal dynamics.*

INTRODUCTION

Ecology stands at the brink of a paradigm shift, where local-scale properties and processes are placed in a broader spatiotemporal framework. In this new “metacommunity” framework, observed pattern and structure are connected across multiple organizational levels (Leibold et al. 2004). The focus of explanations for the maintenance of local species richness has grown to include processes operating at regional scales (Shmida and Wilson 1985, Ricklefs and Schluter 1993). This growth was driven by the need to reconcile seemingly inexplicable patterns at local scales that may be driven by larger scale processes.

I use “space” to refer to processes and patterns observable at different scales (e.g., Holt 1993, Loreau 2000). This differs from the older notion of space in ecology as an explanatory variable in analyses, especially for ordination. This latter use of space is informative and useful, but fails to capture the dynamical nature of space. Many ecological processes are spatially dependent, and others feed back across scales. Further, processes operating across different spatial scales appear necessary to explain patterns of species richness (Whittaker et al. 2001, Amarasekare 2003, Kneitel and Chase 2004, Leibold et al. 2004).

Manuscript received 18 July 2005; revised 10 October 2005; accepted 12 October 2005. Corresponding Editor: M. Holyoak.

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Space as a process appears necessary to understand mechanisms driving ecological dynamics (e.g., James and Shine 2000, Gering and Crist 2002, Chase and Ryberg 2004, Fukami 2004, Cadotte and Fukami 2005, Hamilton et al. 2005). Yet the salient process linking spatial scales is dispersal, and different dispersal patterns can have scale-dependent effects (Drake et al. 1993, Forbes and Chase 2002). Pertinent to any discussion of dispersal and patterns of species richness is the metacommunity concept (Wilson 1992, Cottenie and De Meester 2004, Leibold et al. 2004). I define a metacommunity as local communities of trophically interacting species linked by dispersal. In the current experiment, these local communities occupy discrete resource patches. By connecting local communities, local species richness is thought to be enhanced despite local interspecific interactions that tend to reduce richness (Cottenie and De Meester 2004, Kneitel and Chase 2004). Further, the rate of dispersal is thought to have a nonlinear effect on the magnitude of these richness-reducing interactions, so that richness is maximized at intermediate dispersal rates (e.g., Shurin and Allen 2001, Kneitel and Miller 2003, Mouquet and Loreau 2003). At extremely low dispersal rates, competitive exclusion limits local membership, while at high rates, local communities are homogenized with a suite of dominant competitors maintained in every patch (e.g., Mouquet and Loreau 2003).

The manner in which dispersal influences richness is simply too complex to be captured in a rate function alone. I posit that there are at least two additional processes influencing how dispersal affects richness. First, spatial arrangement of patches may affect the manner in which dispersal influences community structure (Cottenie et al. 2003). Secondly, historical stochastic colonization is known to play an important role in local community structure (e.g., Drake 1991, Law and Morton 1993, Price and Morin 2004) and likely alters the among-community dispersal effect on species richness.

This study examined how dispersal rate, spatial scale of dispersal, and initial local community composition affected species richness at different spatial and temporal scales. I examined three scales of dispersal. In the first, organisms have global dispersal to all other communities; in the second, organisms are restricted to local dispersal only; and in the third, an intermediate-dispersal scale is examined (Fig. 1). If local communities are largely structured by species interactions at the local level then dispersal at a local scale may impede movement through a metacommunity. However, if dispersal rate is high enough, then perhaps species interactions are determined at larger spatial scales so that the dispersal scale is unimportant. Given these mechanisms, a number of hypotheses follow: (1) low-dispersal communities should maintain greater local richness than high-dispersal communities (e.g., Mouquet and Loreau 2003); while (2) local-dispersal metacommunities should maintain higher beta richness than global-dispersal ones; and (3) initial community assembly should have long-term consequences; specifically, that initial variation should maintain higher beta richness; and finally (4) these processes should have interactive effects such that dispersal rate may exhibit different patterns at the different dispersal scales.

METHODS

Landscape and dispersal treatments

Local patches were 125-mL Nalgene narrow-mouth square bottles (Nalg Nunc, Rochester, New York, USA) with two or four 4.76-mm holes drilled into opposing sides and tapped. Threaded 4.76-mm barbed nylon tube fittings (Small Parts, Miami Lakes, Florida, USA) were then twisted into the holes and secured with silicone caulk. A concern was that the number of tube connectors in a local community would alter the surface area for bacterial growth (i.e., protozoan food resources). However, a preliminary experiment found no significant differences in protozoan abundances attributable to the number of connectors. Dispersal corridors were clear Nalgene 4.76-mm tubing. All microcosms were autoclaved prior to use.

The metacommunity designs used in this experiment (Fig. 1) were categorized as: (1) "global," with all communities interconnected and organisms having equal probability of migrating to any other community; (2) "local," in which species in any community can

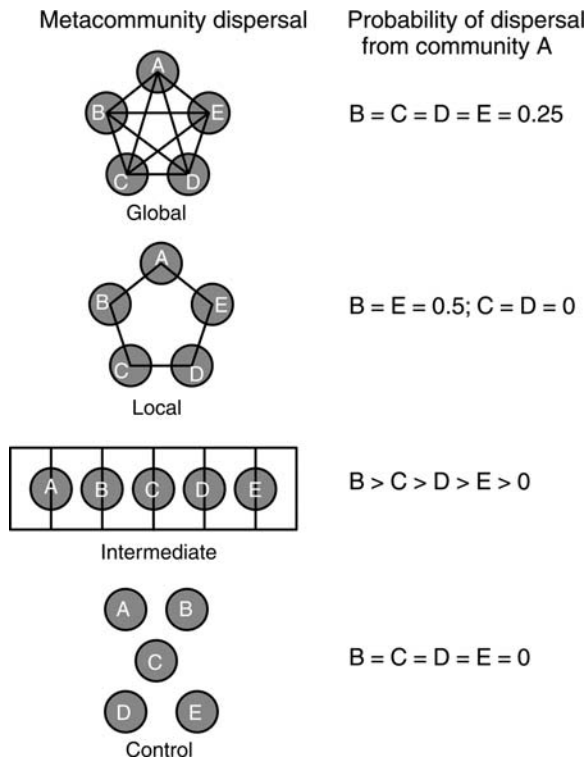


FIG. 1. Dispersal scale designs and the relative probabilities of species dispersal from community A to the other communities (B–E) in the metacommunity.

disperse only to the two neighboring communities; (3) "intermediate," in which organisms do not have equal probability of dispersing to other communities; and (4) the no-dispersal control (Fig. 1). Total length of dispersal pathways was equal between the landscapes, with the control having tubes cut in half and the ends clogged with silicone.

Dispersal rate was manipulated by placing tube clamps on every tube exiting the local communities, and when closed most movement of fluid and organisms was blocked. Three dispersal treatments were used: high dispersal, in which clamps are always open (except during sampling and nutrient renewal); low dispersal, in which clamps are open for one hour every other day; and a no-dispersal control.

Initial community assembly was divided into two treatments. (1) Each species in the species pool (see *Methods: Biological communities*) was initially present in each community and thus initial beta richness was 0. (2) Seven of the 13 species used were initially randomly introduced into each local community, with a beta of 6. In this treatment, all 13 species were present at the metacommunity scale, and the assemblage making up each of the five local communities was repeated for each treatment and replicate (e.g., community A in Fig. 1 was identical for all treatments). All species were recorded on at least one sampling date after initialization. Beta values

were the values for the additive partition of the among-species richness (see *Methods: Statistical analyses*).

Dispersal, landscape design, and initial composition were combined in a factorial design, except in the case of no dispersal, in which landscape design would have no effect. Treatments were replicated four times. One replicate from the high-dispersal/intermediate/initial-beta-0 design was removed due to fungal contamination.

Biological communities

Each local patch consisted of 100 mL of sterilized nutrient medium with 0.55 g/L of protozoa pellets (Carolina Biological Supply, Burlington, North Carolina, USA), 0.05 g/L powdered vitamins, and two sterilized wheat seeds as a source of slowly released nutrients in spring water (Crystal Springs, Flowery Branch, Georgia, USA). Six days prior to the initialization of local communities, the stock solution was inoculated with bacteria (*Bacillus cereus*, *B. subtilis*, *Proteus vulgaris*, and *Serratia marcescens*) from stock cultures and with unidentified bacteria from filtered protozoan species stock cultures. Four days before initialization, microflagellates and further associated unidentified bacteria were introduced, which were assumed to have a ubiquitous distribution throughout the experiment. The above procedure was repeated each day for four days with the first replicate of each of the five treatments being initiated on the first day, and so on.

I used a total of 13 protozoan and rotifer species: *Blepharisma americanum*, *Chilomonas* sp., *Coleps* sp., *Colpidium striatum*, *Euplotes* sp., *Lepadella* sp., *Paramecium aurelia*, *P. bursaria*, *P. caudatum*, *Philodina* sp., *Spirostomum* sp., *Tetrahymena thermophila*, and *Uronema* sp. Three species (*Philodina*, *Lepadella*, and *Euplotes*) were cultured from ponds in and around Knoxville, Tennessee, USA, while the rest were obtained from other laboratories and periodically restocked with individuals ordered from Carolina Biological Supply. Initial number of individuals ranged from 25 to 100 per 100 mL to reduce any strong interactions during the initial phase of the experiment.

The species are protozoan flagellates or ciliates, or metazoan rotifers, all of which naturally inhabit still and stagnant ponds. They range in size from 25 to 1000 μm in length (Appendix A). Species were quite variable in their dietary habits (Appendix A). Appendix A graphically portrays this complex food web.

Sampling

Twice per week, all clamps were closed and 5 mL of medium was removed from each local community and replaced with fresh nutrient medium. Every other week the extracted 5 mL was used to record presence/absence of species. (In a previous study, Cadotte and Fukami [2005] found that diversity indices incorporating local abundance did not change conclusions drawn from richness observations.) Up to the entire 5 mL aliquot was scanned for the presence of species.

Statistical analyses

I used Lande's (1996) additive partitioning of richness and measured species richness at three spatial scales: local or alpha richness was the number of species per 5-mL aliquot, averaged over the five local communities in the landscape; regional or gamma richness was total species in the 5-mL aliquots from the five local communities in the landscape; and among-community or beta richness, measured as gamma minus alpha, or species differences among local communities.

Repeated-measures ANOVAs determined whether treatment combinations had a significant effect on species richness across time after day 1 (initial richness). An assumption for the repeated-measures *F* test is that the variance-covariance matrix has compound symmetry. When there was a departure from compound symmetry, I used Greenhouse-Geisser epsilon and its correction where appropriate. However, since the factorial design was unbalanced, interactive effects (other than time) could not be examined using repeated-measures ANOVAs; therefore, I examined single treatment effects. To examine interactive effects, I used multiway ANOVAs for the last sampling day (day 50). ANOVAs were performed using SAS version 9 (SAS Institute, Cary, North Carolina, USA).

To test whether differential dispersal probabilities resulted in observable differences in composition, community similarity was calculated using either the Sorenson index or between-community contrasts within a metacommunity, at day 50. For example, highly connected communities should be more similar than less connected communities. The similarity values were analyzed using a three-way ANOVA with dispersal rate, dispersal pathway, and initial beta as factors.

RESULTS

The 50 days of the experiment, or 50–100 generations of the study organisms, represented long-term dynamics. Some treatment combinations showed very different temporal dynamics at different spatial scales (Fig. 2A). At the local (alpha) level, treatment combination ($F_{13,168} = 6.49$, $P < 0.0001$), time ($F_{3,168} = 49.90$, $P < 0.0001$), and their interaction ($F_{39,168} = 4.54$, $P < 0.0001$) affected species richness. Similarly, beta richness was affected by treatment combination ($F_{13,168} = 15.21$, $P < 0.0001$) and time ($F_{3,168} = 11.25$, $P < 0.0001$), but their interaction was not significant ($F_{39,168} = 1.37$, $P = 0.090$). Regional (gamma) richness was also affected by treatment ($F_{13,168} = 9.86$, $P < 0.0001$), time ($F_{3,168} = 8.40$, $P < 0.0001$), and their interaction ($F_{39,168} = 1.82$, $P = 0.005$). To highlight the variation among treatments, Fig. 2B shows species richness patterns at day 50. Local richness was 5–7 species, while regional richness was 7–11 species.

The three factors manipulated in this experiment all affected species richness at multiple scales across time (see Appendix B), and time also had a highly significant effect ($P < 0.01$ for all tests below). Dispersal rate affected local ($F_{2,212} = 5.67$, $P = 0.0040$), beta ($F_{2,212} =$

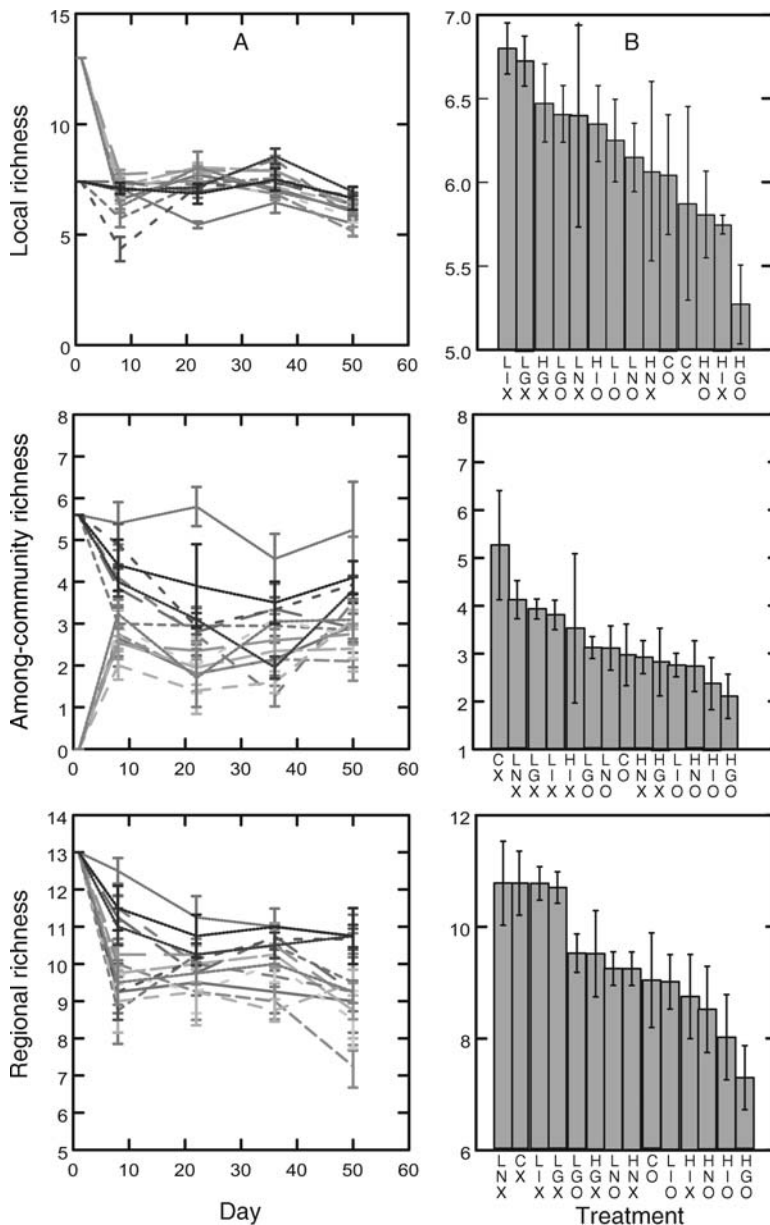


FIG. 2. Local, among-community, and regional richness for the 14 treatments used in the experiment. (A) The full temporal dynamics for the treatments. Treatment labels are not present because of the number of treatments; instead, this figure shows the dynamics and extent of variation among treatment combinations. (B) The treatment effects at day 50, showing the variation among treatment combinations. L and H refer to low- and high-dispersal rates, respectively, and C refers to the no-dispersal control; G, I, and N refer to the global-, intermediate-, and local- (neighbor) dispersal scales, respectively; and O and X refer to initial beta of 0 and 6, respectively. Data are means \pm SE.

10.92, $P < 0.0001$), and regional richness ($F_{2,212} = 5.16$, $P = 0.0065$). Dispersal rate interacted with time to influence species diversity at the local scale ($F_{6,212} = 2.23$, $P = 0.042$), but not at the other scales of observation. Dispersal scale affected local ($F_{3,208} = 11.67$, $P < 0.0001$), beta ($F_{3,208} = 7.82$, $P = 0.0001$), and regional richness ($F_{3,208} = 5.24$, $P = 0.0017$). Dispersal scale interacted with time to influence species diversity at

the local scale ($F_{9,208} = 2.86$, $P = 0.003$), but not at the other scales of observation. Finally, initial beta did not affect local richness ($F_{1,216} = 1.80$, $P = 0.1805$) but did affect beta ($F_{1,216} = 73.99$, $P < 0.0001$) and regional richness ($F_{1,216} = 55.81$, $P < 0.0001$). Initial beta interacted with time to affect diversity at both the local ($F_{3,216} = 7.85$, $P < 0.0001$) and beta ($F_{3,216} = 3.21$, $P = 0.024$) scales, but not at the regional scale.

Generally, for the local community, low dispersal rate and intermediate dispersal scale maintained higher richness over time, with no dispersal or the global dispersal maintaining the lowest richness. A lack of dispersal or initial species variation maintained greater beta diversity, while high dispersal and the global- and intermediate-dispersal scales maintained lower beta richness. At the regional level, the control and low-dispersal treatments as well as initial beta diversity of 6 maintained the highest richness, while high dispersal and the all pathway maintained lower richness.

Species richness values at day 50 were mainly consistent with the results of the repeated-measures ANOVAs. Dispersal affected local ($F_{2,50} = 6.35$, $P = 0.0035$), beta ($F_{2,50} = 6.11$, $P = 0.0042$), and regional richness ($F_{2,50} = 5.30$, $P = 0.0082$). In all cases, a high dispersal rate adversely affected richness (Fig. 3). Initial beta had no effect on local richness ($F_{1,50} = 0.69$, $P = 0.4086$), but did affect beta ($F_{1,50} = 17.29$, $P = 0.0001$) and regional richness ($F_{1,50} = 18.20$, $P < 0.0001$). On day 50 an initial beta of 6 led to higher richness at the end of the experiment than initial beta of 0 (Fig. 3). However, contrary to the repeated-measures ANOVAs, dispersal scale had no direct effects on richness at any scale of observation at day 50.

However, there were some important interactive effects (Figs. 3 and 4). The effect of dispersal on local richness depended on initial beta ($F_{2,50} = 3.94$, $P = 0.0257$). With initial beta 6, dispersal produced a unimodal richness pattern (Fig. 3), while dispersal had no effect with an initial beta of 0. With initial beta of 6, beta richness showed a monotonic decline with increasing dispersal, but again there was no relationship when initial beta was 0 (Fig. 3). Interestingly, despite interactions at the local and among-community (beta diversity) scales, there was no interaction between initial beta and dispersal for regional diversity (Fig. 3).

Dispersal scale appeared important in a three-way interaction with the other factors (Fig. 4). In the global-dispersal-scale metacommunity, with initial beta 0 and high dispersal, species richness was the lowest. However, if initial beta was 6, then richness was no different than the other dispersal rate and scale treatments. While in the intermediate dispersal scale, the treatment combination resulting in the lowest richness was high dispersal with initial beta 6.

Community similarity

Mean community similarity was significantly affected by dispersal rate ($F_{1,448} = 28.64$, $P < 0.0001$), dispersal scale ($F_{2,448} = 9.83$, $P < 0.0001$), and initial beta ($F_{1,448} = 34.69$, $P < 0.0001$; Fig. 5). Contrary to the prediction, the intermediate-dispersal scale showed greater similarity than all other dispersal-scale treatments (Fig. 5A). There was also a significant interaction between dispersal rate and initial beta ($F_{1,448} = 6.26$, $P < 0.013$; Fig. 5B). As expected, a higher dispersal rate and initial beta of 0 resulted in greater similarity (Fig. 5B).

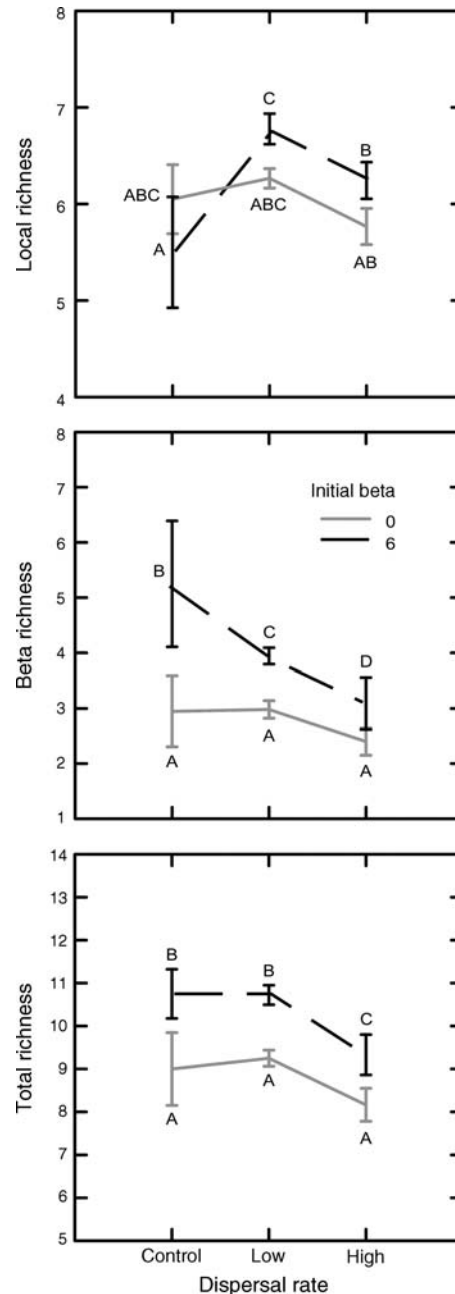


FIG. 3. The effects of dispersal rate and initial beta (0 vs. 6) on local, beta, and regional richness on day 50 (means \pm SE). Different uppercase letters refer to significant differences at $P < 0.05$.

Species occupancy

The occupancy of more than half of the species used in this experiment was affected by at least one treatment (Table 1). The dispersal rate and initial-beta results highlighted the importance of adverse species interactions, but the pathway treatment was more difficult to interpret. Of the seven species whose occupancy was significantly affected by dispersal rate, four (*Blepharisma*, *Colpidium*, *Euplotes*, and *Philodina*) had higher

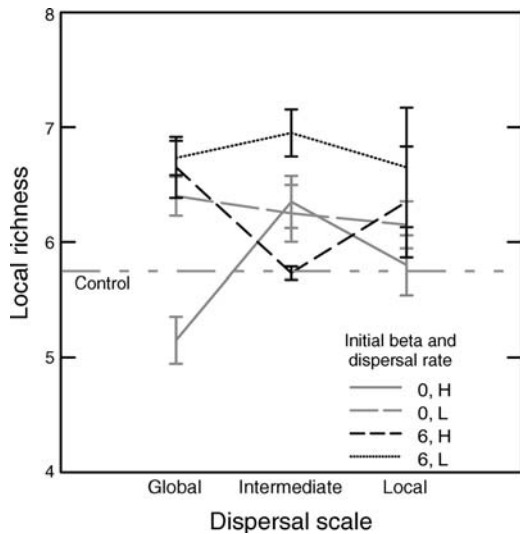


FIG. 4. The effect of the three-way interactions among dispersal scale, initial beta (0 vs. 6), and dispersal rate (L, low; H, high) on local richness on day 50 (means \pm SE).

occupancy in the presence of dispersal, and three species (*Chilomonas*, *Coleps*, and *Tetrahymena*) maintained higher occupancy in the no-dispersal control (Appendix C). Of the nine species affected by initial beta, five (*Blepharisma*, *Coleps*, *Euplotes*, *Paramecium bursaria*, and *Philodina*) had higher occupancy when they were initialized in all local communities. However, the other four species (*Chilomonas*, *Paramecium caudatum*, *Spirostomum*, and *Tetrahymena*) maintained higher occupancy, and therefore lower extinction rates, when there was initial variation in local-species composition (Appendix C). Two species (*Chilomonas* and *Spirostomum*) had their lowest occupancies in the global-dispersal metacommunities. Two other species (*Colpidium* and

Philodina) had their highest occupancy at the intermediate-dispersal scale (see Appendix C).

DISCUSSION

The objective of this experiment was to examine the manner in which dispersal rate between patches in a metacommunity, dispersal scale, and initial species composition influenced levels of partitioned diversity. The results appeared to be more complicated than the predictions for two reasons. First, the relative strengths of dispersal rate, scale, and initial composition on species richness could not be determined a priori. Second, the different species had species-specific responses to the treatments used.

A potential hypothesis would have been that better dispersers persist longer and occupy more patches in the interconnected communities because they can move to avoid superior competitors. Further, in metacommunities with initial compositional variation there may be local assemblages with open niches for allowing these dispersers to invade. Dispersal abilities (M. W. Cadotte, D. V. Mai, S. Jantz, M. Keele, and J. A. Drake, unpublished manuscript; see Table 2) were not related to species occupancy patterns (binomial probabilities $>$ 0.05). Generally, species that either negatively responded to dispersal or positively responded to initial variation were most likely to go extinct in the global-dispersal-scale treatment. These competitively inferior species likely find temporary refuges in the initial absence of large populations of superior competitors.

The relative effect of dispersal rate, scale, and initial beta on richness depends on the spatial scale of interest. If our concern is to maximize local richness, then a low dispersal rate and an intermediate dispersal scale best enhanced richness (Mouquet and Loreau 2003). However, if we are concerned with metacommunity richness, then low or no dispersal maintained the highest richness. Further, having

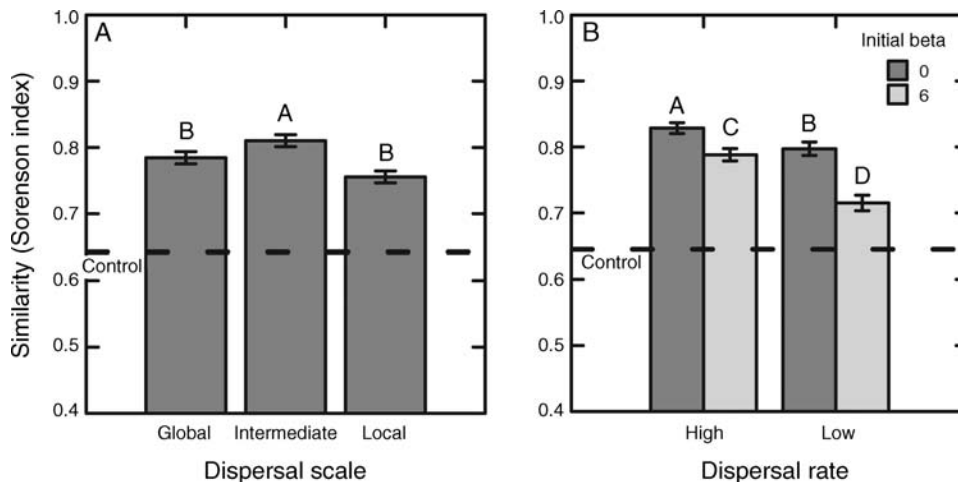


FIG. 5. Community similarity on day 50 as affected by (A) dispersal scale and (B) both dispersal rate and initial beta, which also reveals the interaction between these two factors (means \pm SE). Different uppercase letters above bars refer to significant differences ($P <$ 0.05).

TABLE 1. Results of repeated-measures ANOVAs testing the effect of dispersal rate, pathway, and initial beta on the number of patches occupied by each species.

Species	Dispersal rate			Pathway			Initial beta			Time trend†
	F	df	P	F	df	P	F	df	P	
<i>Blepharisma americanum</i>	19.00	2, 202	0.0001***	12.23	2, 198	0.0001***	19.00	2, 206	0.0001***	increases
<i>Chilomonas</i> sp.	9.13	2, 202	0.0002***	7.68	2, 198	0.0001***	26.09	2, 206	0.0001***	declines
<i>Coleps</i> sp.	7.75	2, 202	0.0006**	4.54	2, 198	0.0042*	13.57	2, 206	0.0001***	declines
<i>Colpidium striatum</i>	11.33	2, 202	0.0001***	8.06	2, 198	0.0001***	0.38	2, 206	0.539	unimodal
<i>Euploes</i> sp.	4.69	2, 202	0.0102*	3.83	2, 198	0.0107*	5.07	2, 206	0.0254	declines
<i>Lepadella</i> sp.	0.94	2, 202	0.391	2.85	2, 198	0.0388	3.55	2, 206	0.0774	increases
<i>Paramecium aurelia</i>	2.01	2, 202	0.136	2.13	2, 198	0.0976	0.47	2, 206	0.493	declines
<i>Paramecium bursaria</i>	0.37	2, 202	0.693	0.72	2, 198	0.539	91.68	2, 206	0.0001***	increases
<i>Paramecium caudatum</i>	1.65	2, 202	0.195	3.85	2, 198	0.0103*	29.95	2, 206	0.0001***	declines
<i>Philodina</i> sp.	5.53	2, 202	0.0046*	6.77	2, 198	0.0002***	112.18	2, 206	0.0001***	increases
<i>Spirostomum</i> sp.	1.17	2, 202	0.311	7.25	2, 198	0.0001***	118.46	2, 206	0.0001***	increases
<i>Tetrahymena thermophila</i>	3.69	2, 202	0.027	2.65	2, 198	0.051	4.85	2, 206	0.0287	declines
<i>Uronema</i> sp.	0.62	2, 202	0.538	0.93	2, 198	0.425	5.41	2, 206	0.021	concave

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, all after Bonferroni correction (graphs are shown in Appendix C).

† Time was significant for all species repeated-measures ANOVAs.

initial compositional variation among local communities enhanced metacommunity, but not local, richness.

Few studies have explicitly examined the scale and rate of dispersal and its effects on diversity at different spatial scales (but see Forbes and Chase 2002, Cottenie et al. 2003, Cadotte and Fukami 2005). Whereas numerous studies show that dispersal generally affects local diversity (Warren 1996, Tilman 1997, Gilbert et al. 1998, Shurin 2001, Kneitel and Miller 2003, but see Pärtel et al. 1998), results are mixed on whether spatial configuration is important (Holyoak 2000, Forbes and Chase 2002, Cottenie et al. 2003, Cadotte and Fukami 2005). The large effects of dispersal rate at multiple spatial scales are not surprising (Forbes and Chase 2002, Cottenie and DeMeester 2004). Some studies have shown strong local community effects (Kneitel and Miller 2003) and others strong regional effects (Forbes and Chase 2002, Cadotte and Fukami 2005). Interestingly, other studies have not found strong community effects of scale of dispersal (e.g., Forbes and Chase 2002, Cadotte and Fukami 2005). However, Cottenie et al. (2003) found, in

a natural metacommunity of interconnected ponds, that spatial configuration created metacommunity structure (differences among local communities). They showed that these differences could not be explained by environmental differences alone. The current results reveal that for species diversity, configuration can have important interactive effects with other processes (Fig. 4) or counterintuitive effects (Fig. 5A).

Cottenie and De Meester (2004) see metacommunities as the interplay between environmental variation driving divergence in composition and dispersal promoting convergence. Metacommunities are likely structured in a more complicated fashion. The configuration effects in Cottenie et al. (2003) and the current study reveal that patch spatial arrangement or scale of dispersal can serve as a source of intrinsic metacommunity structure. From the current results, I would posit that a third axis be added to Cottenie and De Meester's scheme, namely variation in species interactions, which is the product of stochastic compositional variation created by community assembly dynamics (e.g., Fukami 2004). Interaction

TABLE 2. Mean time to colonize four other patches in a single-species metacommunity ($n = 3$ trials) and the corresponding dispersal rank.

Species	Mean dispersal time (wk) (SD)	Dispersal rank	Dispersal rate effect	Initial beta effect
<i>Blepharisma americanum</i>	2.67 (0.58)	9	+	—
<i>Chilomonas</i> sp.	2.00 (0.00)	4.5	—	+
<i>Coleps</i> sp.	2.00 (0.00)	4.5	—	—
<i>Colpidium striatum</i>	1.00 (0.00)	2	+	NS
<i>Euploes</i> sp.	2.00 (0.00)	4.5	+	—
<i>Lepadella</i> sp.	4.67 (0.58)	12	NS	NS
<i>Paramecium aurelia</i>	2.00 (0.00)	4.5	NS	NS
<i>Paramecium bursaria</i>	3.00 (0.00)	10.5	NS	—
<i>Paramecium caudatum</i>	3.00 (0.00)	10.5	NS	+
<i>Philodina</i> sp.	5.33 (1.16)	13	+	—
<i>Spirostomum</i> sp.	2.33 (0.58)	7	NS	+
<i>Tetrahymena thermophila</i>	1.00 (0.00)	2	—	+
<i>Uronema</i> sp.	2.67 (1.16)	9	NS	NS

Notes: The final two columns give the sign of the effect of dispersal rate (“+” refers to increased occupancy with dispersal) and initial beta (“+” refers to increased occupancy with initial beta of 6; see Appendix C). “NS” refers to a nonsignificant treatment effect. Data are from M. W. Cadotte, D.V. Mai, S. Jantz, M. Keele, and J. A. Drake (*unpublished manuscript*).

variation seems to promote long-term, large-scale effects on community similarity and patterns of richness by maintaining divergence among local communities.

The role of establishment history in this experiment is surprising and important. The large difference among the global-dispersal-scale treatments reveals that even under high homogenizing pressure, local-community compositional variation remained intact and likely resisted some species invasions (e.g., Drake et al. 1993, cf. Chase 2003). Shurin (2001) showed, in a pond system, that saturated local communities could essentially resist the invasion of new individuals. The effects of colonization history were most apparent at the beta and regional scales in this experiment. Several studies (Drake 1991, Law and Morton 1993, Price and Morin 2004) revealed that colonization history can be very important for local, closed communities. The current results reveal that these initial local differences can have profound effects even when communities remain open to immigration and at larger spatial scales (Fig. 3). Further, the successional and temporal dynamics, which in large part were affected by immigration, were highly impacted by the initial assembly (Mouquet et al. 2003, Fukami 2004). Most importantly, the presence of initial compositional variation determined whether these results supported or refuted an important metacommunity hypothesis. Mouquet and Loreau (2003) used a model to show that local richness should be maximized at intermediate-dispersal rates, while beta and regional richness should decline. I was able to confirm this when there was initial compositional variation, but failed to support it without this variation (Fig. 3). With all competitors initially present, the benefits of dispersal seem to be greatly diminished.

There are a number of field situations in which initial community assembly is an important aspect of community temporal dynamics. Post-disturbance assembly (Brotons et al. 2005), habitat restoration (Young et al. 2001), and species invasions (Wilson et al. 2000) are all examples of local habitat assembly. Further, the trend towards widespread agricultural abandonment in Europe and Eastern North America (Flinn and Vellend 2005) means that there may be large-scale and long-term consequences to local assembly dynamics in patchy landscapes. Jacquemyn et al. (2001) showed that patch area, age, and dispersal limitation were all-important for local patterns of richness in a fragmented landscape. Their study showed that long-term consequences were measurable for at least 223 years after field abandonment (the age of the oldest patches).

It is important to note that not all species benefit from dispersal (e.g., Burkey 1997, Cadotte and Fukami 2005), and in fact richness may be negatively impacted by dispersal (Mouquet and Loreau 2003; cf. Brown and Kodric-Brown 1977, Shmida and Wilson 1985). The species used in this experiment varied in their responses to immigration, no doubt driven by specific interactions with the other species in the metacommunity. Experiments also using protozoan microcosms have found that

dispersal can either increase the persistence of species (Holyoak and Lawler 1996) or increase the extinction risk (Burkey 1997, Cadotte and Fukami 2005) depending on the nature and stability of the interactions.

Conclusions

Ecologists often suppose that local and regional processes are important processes structuring richness (e.g., Ricklefs 1987, Cornell and Lawton 1992). However, the current results reveal that dispersal likely has different effects on richness at different spatial scales and not as a single "regional" process. Instead, dispersal is a process at the "mesoscale" (Holt 1993), interacting with processes and community composition at a number of spatial scales. Further, assuming that dispersal generally has a positive effect on species richness ignores potential negative species-specific responses to invading competitors (Mouquet and Loreau 2003). How any specific system responds to larger-scale processes, individual species, and community responses should be ascertained to determine the negative and positive impacts.

ACKNOWLEDGMENTS

I acknowledge helpful advice from Jim Drake, Bob Holt, Aaron King, Dan Simberloff, Nathan Sanders, and the community ecology discussion group at the University of Tennessee and to Karl Cottenie, Jim Drake, and an anonymous reviewer for helping to greatly improve the quality of this manuscript. Invaluable laboratory help was provided by Kristin Clark, Sam Jantz, Monica Keele, and Donny Mai. I am indebted to financial support from the department of Ecology and Evolutionary Biology, Science Alliance and Scholarly Activity and Research Incentive Funds, all at the University of Tennessee.

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APPENDIX A

A table and a figure describing the biological community of this study (*Ecological Archives* E087-058-A1).

APPENDIX B

A figure showing temporal richness trajectories for dispersal rate, dispersal pathway, and initial beta at three spatial scales (*Ecological Archives* E087-058-A2).

APPENDIX C

Figures showing single species responses to experimental treatments (*Ecological Archives* E087-058-A3).