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LETTER

Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape

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Abstract

Although there has been growing interest in the effect of dispersal on species diversity, much remains unknown about how dispersal occurring at multiple scales influences diversity. We used an experimental microbial landscape to determine whether dispersal occurring at two different scales – among local communities and among metacommunities – affects diversity differently. At the local scale, dispersal initially had a positive effect and subsequently a neutral effect on diversity, whereas at the metacommunity and landscape scales, dispersal showed a consistently negative effect. The timing in which dispersal affected beta diversity also differed sharply between local communities and metacommunities. These patterns were explained by scale- and time-dependent effects of dispersal in allowing spread of species and in removing spatial refuges from predators. Our results suggest that the relative contribution of opposing mechanisms by which dispersal affects diversity changes considerably over time and space in hierarchical landscapes in which dispersal occurs at multiple scales.

Keywords

Competition, hierarchy, metacommunity, microcosms, predation, spatial ecology, spatial refuge, species coexistence, succession, transient dynamics.

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> 'A real environment has a hierarchical structure. That is to say, it is like a checkerboard of habitats, each square of which has, on close examination, its own checkerboard structure of component subhabitats. And even the tiny square of these component checkerboards are revealed as themselves checkerboards, and so on.' (MacArthur 1972: 186)

INTRODUCTION

Recent studies have suggested that different ecological processes influence the coexistence of species and the maintenance of diverse communities differentially at different spatial scales (e.g. Gonzalez *et al.* 1998; Bond & Chase 2002; Chase & Leibold 2002; Gering & Crist 2002; Maurer & Taper 2002). A primary theme of these studies has been interactive effects of two processes: interspecific interactions, particularly competition and predation, as a local process and dispersal of individuals across local communities as a regional process (e.g. Ricklefs 1987; Srivastava 1999; Shurin & Allen 2001; Hillebrand & Blenckner 2002). Integrating dispersal into the conceptual framework for species diversity, which traditionally focused on local processes, has led to a greater understanding of local and regional species diversity (Leibold *et al.* 2004).

However, how dispersal structures communities has proven difficult to understand, because dispersal can have opposing effects on species coexistence. On the one hand, dispersal can increase local species diversity through rescue effects, by which colonists from other communities re-establish local populations that have gone extinct (Brown & Kodric-Brown 1977; Hanski 1999), and through source-sink effects [also known as mass effects (Schmida & Ellner 1984)], by which supply of immigrants sustains local populations that would otherwise have a negative net growth (Pulliam 1988; Loreau & Mouquet 1999; Amarasekare & Nisbet 2001). On the other hand, dispersal can also decrease local diversity by reducing effects of spatial refuges, or subdivided habitats that act as refuges for species that are competitively inferior or highly vulnerable to predation (Horn & MacArthur 1972; Hastings 1980; Holyoak & Lawler 1996; Chesson 2000; Kneitel & Miller 2003). Predicting the effects of dispersal at larger spatial scales is even more difficult (Kneitel & Chase 2004). Dispersal may

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lead to regional homogenization of local community structure, or decreased beta diversity, which may in turn lead to decreased regional diversity. However, whether regional diversity is increased or decreased by dispersal depends not only on beta diversity, but also on the magnitude of dispersal-induced changes in local diversity (Gering & Crist 2002).

One aspect of dispersal that received little attention by recent studies is the hierarchical nature of habitats (but see Allen & Starr 1982; O'Neill *et al.* 1986; Kotliar & Wiens 1990; Lavorel *et al.* 1993; Kolasa & Waltho 1998). While viewing dispersal as a regional process has proved to be useful, dispersal occurs over a wide range of spatial scales, rather than at one particular 'regional' scale. As MacArthur (1972; quoted above) and a number of others pointed out, many ecosystems have a hierarchical structure containing multiple levels of spatial organization (Kotliar & Wiens 1990). Few studies have explicitly considered the role of dispersal at more than one spatial scale in determining species diversity in the presence of interspecific interactions (Kolasa *et al.* 1996). Whether dispersal affects diversity positively or negatively may depend on the spatial scale at which dispersal occurs, the spatial scale at which diversity is observed, and interaction of the two, but these possibilities largely remain to be experimentally tested.

Another aspect of dispersal that has often been ignored is the role of transient community dynamics in understanding species diversity. Most conceptual models of local communities and metacommunities assume that communities achieve equilibrium over ecological time scales (Leibold *et al.* 2004). While these models are conceptually valuable, many natural communities rarely reach an equilibrial state and instead show long-term transient dynamics. Theory suggests that transient dynamics can explain coexistence of species when equilibrium-based models predict otherwise (DeAngelis & Waterhouse 1987; Hastings 2004). During transient dynamics, the relative importance of negative and positive effects of dispersal on diversity may change over time, as is suggested by succession theory (e.g. Walker & Chapin 1987), but there have been few experimental tests of these ideas.

These issues involving multiple spatial and temporal scales and multiple species are extremely difficult to study in the field because of the amount of effort required to manipulate dispersal and to measure species diversity in sufficient scope and detail. One approach that has proven powerful is the use of controlled microbial microcosms as an empirical model system (Drake *et al.* 1996; Morin 1998; Jessup *et al.* 2004; Cadotte *et al.* 2005). Although the advantages of laboratory microcosms come at the sacrifice of a natural context (Carpenter 1996; Morin 1998), they are nevertheless useful for refining the hypotheses to test in more natural, but longer, larger-scale, and more expensive field experiments (Morin 1998; Cadotte *et al.* 2005). In this paper, we report a laboratory study that used experimental microcosmic landscapes aggregating local communities into metacommunities. Our goal was to determine whether dispersal at two spatial scales – among local communities and among metacommunities – can affect species diversity differently depending on the spatial scale and timing of observation. We observed community dynamics at three scales: local communities, metacommunities and landscapes.

MATERIALS AND METHODS

Landscape establishment and dispersal treatment

The experimental topology we used was a tri-tiered hierarchical assemblage of three local communities comprising a metacommunity and three metacommunities comprising a landscape, with three dispersal treatments (Fig. 1). In treatment I, the three local communities in each metacommunity were linked by dispersal, as were the three

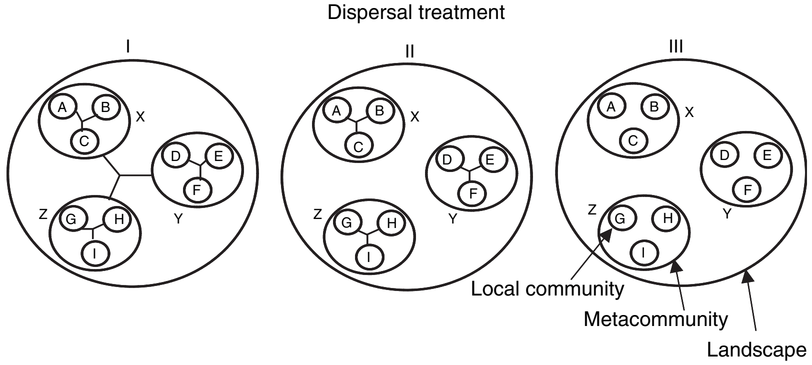

Figure 1 Schematic representation of three dispersal treatments. A–I represent local communities, X–Z represent metacommunities, and the lines attaching local and metacommunities represent dispersal treatments.

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metacommunities. In treatment II, only the three local communities within each metacommunity were dispersal linked. In treatment III, there was no dispersal linkage. Each treatment was replicated four times, resulting in a total of 12 landscape replicates (3 treatments × 4 replicates per treatment).

Dispersal in landscape I was carried out by removing 3 mL from all nine local communities and redistributing among the local communities. Therefore, by carrying out this between-metacommunity dispersal, we were implicitly carrying out within-metacommunity dispersal simultaneously. Dispersal in landscape II was conducted by removing 3 mL from each of the three local communities within each metacommunity and returning 3 mL from the homogenized mixture to each local community within that metacommunity. We performed the dispersal treatments every 3.5 days (i.e., every third and seventh day), which corresponds to about 1.5 to 4 generations of the organisms involved, allowing enough time for inter-dispersal dynamics. Lasting for 17 weeks (see below), our experiments followed community dynamics for about 60–120 generations. Although our dispersal treatment is analogous to proportional sampling and is necessarily simplified, our methods allow for a strong test of whether hierarchical structuring of communities through dispersal affects diversity even in the absence of differential dispersal rates and ecological tradeoffs. Our dispersal treatment is based on Warren's (1996a,b) approach, which successfully tested metacommunity theory using a protist microcosm.

It should be noted that we did not have a treatment in which dispersal occurred only between metacommunities and not between local communities. We failed to see biological significance of such a treatment. Further, in this experiment, we did not address potentially important effects of more frequent dispersal at smaller spatial scales. We also did not study effects of variation in species composition between metacommunities. We will discuss these and other related issues in the future directions section in Discussion.

Each local community consisted of a loosely covered 250-mL glass jar filled with 100 mL of nutrient solution (80 mL of stock solution plus 20 mL from initial species additions), with 0.55 g L^{-1} of protozoa pellets (Carolina Biological Supply Company, Burlington, NC, USA), 0.05 g L^{-1} powdered vitamins, and two sterilized wheat seeds as a source of slowly released carbon, in commercially available spring water (Crystal Springs, DS Waters of America, Atlanta, GA, USA). Five days prior to the initialization of local communities, the stock solution was inoculated with four bacterial species (*Bacillus cereus*, *Bacillus subtilis*, *Proteus vulgaris*, *Serratia marcescens*) and with unidentified bacteria from filtered bacterivorous species cultures in order to introduce bacterial species that would subsequently be introduced with the bacterivores. Three days before landscape initialization, microflagellates were introduced. The above procedure was repeated each day for 6 days, and two landscapes were initialized on each day (treatment I replicate 1 and II-1 on day 1, III-1 and I-2 on day 2, and so on), so that 18 local communities (or two landscapes) were sampled on a given day.

We used a total of 14 protozoan and rotifer species. Eleven of these species were bacterivores, whereas the rest were predators of the bacterivores (Table 1). Some of the bacterivorous species also fed on microflagellates. Each local community was initialized with 10 species (eight bacterivores and two predators) in order to introduce baseline variation in species composition among local

Table 1 Species used in this experiment

Species	Trophic level	Approximate initial density	Initial communities
Didinium sp.	Predator	20 cells	A, B, D, E, G, H
Lacrymaria sp.	Predator	20 cells	A, C, D, F, G, I
Stentor coeruleus	Predator	20 cells	B, C, E, F, H, I
Chilomonas sp.	Bacterivore	3.9×10^4 mL^{-1}	ALL
Colpidium striatum	Bacterivore	2.7×10^3 mL^{-1}	ALL
Colpoda cucullus	Bacterivore	3.5×10^3 mL^{-1}	A, B, C, D, F, H
Colpoda inflata	Bacterivore	7.5×10^3 mL^{-1}	B, C, E, G, H
Lepadella sp.^{r}	Bacterivore (also consumes microflagellates)	4.0×10^2 mL^{-1}	B, C, D, E, F, G
Paramecium caudatum	Bacterivore (also consumes microflagellates)	100 mL^{-1}	C, D, F, G, I
Paramecium tetraurelia	Bacterivore	6.8×10^2 mL^{-1}	A, B, C, D, E, F, H, I
Rotaria sp.^{r}	Bacterivore (also consumes microflagellates)	3.4×10^2 mL^{-1}	A, E, G, H, I
Spirostomum sp.	Bacterivore	105 mL^{-1}	A, B, E, H, I
Tetrahymena thermophila	Bacterivore	3.0×10^3 mL^{-1}	ALL
Uronema sp.	Bacterivore	3.0×10^3 mL^{-1}	A, C, D, F, G, I

Rotifers are marked with^r. All other species are protozoa.

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communities. Initial local community composition was constrained by the following three rules. First, the three local communities in a metacommunity must contain the three possible combinations of two predators. Second, bacterivorous species in predator cultures had to be included in all communities to reduce the impact of species contamination. These species were *Chilomonas* sp., *Colpidium striatum* and *Tetrahymena thermophila*. Third, the other bacterivorous species were chosen using a random number table, given that all species were in at least one local community in each metacommunity. The exact same local species assemblages were used in each dispersal treatment and each replicate. For example, the initial species composition of community A in treatment I was identical to that of community A in treatments II and III (Fig. 1).

Sampling

Once a week, 6 mL of medium was removed from each local community and replaced with fresh medium with the same constituent concentration detailed above. Throughout the experiment, we did this medium replacement immediately before a dispersal treatment. On sampling dates, this 6 mL was used as the source for the sample. We performed two types of sampling procedures: individual-based counts and presence/absence sampling. The individual-based counts were performed four times, first at time 0 to get initial densities being introduced into the communities, and at weeks 6, 11 and 17. On these dates, we counted all individuals of each species in a 0.2-mL subsample. If species densities were too high to be accurately estimated, we diluted the sample by adding 2 mL of bacterized solution and counted all individuals in a 0.2 mL subsample of the dilution. We scanned the remaining 6 mL aliquot for species not observed in the 0.2 mL sample. These low-density species were enumerated for the entire 6 mL sample. Presence/absence sampling was performed seven times, at weeks 1, 3, 5, 8, 10, 13 and 15 (with additional three data points from the individual-based counts). For this sampling we removed a 0.2-mL subsample for ease of observation and recorded all species present. We also scanned the entire 6 mL aliquot for the presence of low-density species. Our previous experience suggested that scanning a 6-mL sample rarely missed a species present in our microcosms.

We measured species richness at three spatial scales of observation: local community (i.e. number of species observed in the 6-mL aliquot, averaged over the nine local communities in the landscape), metacommunity (i.e. total number of species observed in the 6-mL aliquots from the three local communities within a metacommunity, averaged over the three metacommunities in the landscape), and landscape (i.e. total number of species observed in the 6-mL aliquots from the nine local communities in the landscape). We also examined beta diversity, or community dissimilarity, at both local community and metacommunity scales. Beta diversity was calculated by subtracting mean species richness at the local community scale or at the metacommunity scale from total species richness at the landscape scale (Lande 1996).

Statistical analyses

We used repeated measures ANOVA and Tukey's *post hoc* tests to determine if dispersal treatments had a significant effect on species richness across time. An assumption for the repeated measures *F*-test is that the variance–covariance matrix has compound symmetry. When there was departure from compound symmetry, we used Greenhouse-Geisser Epsilon and its correction where appropriate. We used SAS version 8.02 (SAS Institute 2001) for the ANOVAs and produced all other statistics and graphs using SYSTAT version 10 (SPSS Inc. 2000). For species richness at the landscape scale, we log-transformation the data (to normalize Poisson distributed errors) and found the same results as for non-transformed data. In addition to species richness, we used Simpson's diversity index (Lande 1996) as another measure of species diversity. We found that Simpson's diversity gave the same patterns as species richness (data not shown).

We also examined the frequency (proportion of the local communities where the species was recorded) of individual species to search for mechanisms responsible for dispersal effects on diversity. We compared the frequency of each species (i) among dispersal treatments, (ii) between local communities where the focal species was initially present versus absent, and (iii) between local communities where a generalist predator, *Stentor coeruleus*, was initially present vs. absent. We focused on effects of *Stentor* because it became evident during the experiment that *Stentor* was structuring local community composition to a greater degree than any other species (see below).

We further examined the effect of predators on prey community composition using a Mantel test at each sampling date. Mantel test correlates the distance matrix of dissimilarities among local prey communities (composition and abundance) to distance matrix of predator composition and abundance. We constructed the distance matrices using the Sørensen distance measures (McCune & Grace 2002). The Mantel test produces a test statistic *r*, which is analogous to a Pearson correlation coefficient, as well as a *Z*-statistic used for significance testing (McCune & Grace 2002). To determine significance we compared the observed *Z* statistic to a distribution created by random Monte Carlo permutations, with 1000 randomizations. We did this test using PC-ORD for Windows (MjM Software, Gleneden Beach, OR, USA).

One replicate of treatment III had to be discarded from analysis because of an erroneous dispersal treatment carried out in week 3. We detected no other systematic contamination.

RESULTS

Species richness

Species richness declined over time at all scales of observation, but the rate of decline differed greatly between the three scales (Fig. 2a–c). Dispersal among local communities significantly affected species richness (compare treatments II and III in Fig. 2a–c), whereas dispersal among metacommunities had no significant effects on richness (compare treatments I and II in Fig. 2a–c).

Dispersal among local communities had a marginal effect on local species richness ($F = 4.20$, $P = 0.0565$), with increased species richness in the dispersal treatments during weeks 3, 5 and 15 (Fig. 2a). Dispersal among local communities had a much stronger effect on richness at the metacommunity scale ($F = 13.29$, $P = 0.003$; Fig. 2b) and at the landscape scale ($F = 18.77$, $P < 0.001$; Fig. 2c). At both scales, dispersal among local communities decreased species richness from week 5 to week 13. The significant differences between dispersal treatments had disappeared by the end of the experiment.

Dispersal among local communities decreased beta diversity at both local community and metacommunity scales during much of the experiment (Fig. 2d,e). However, the timing in which dispersal significantly affected beta diversity depended on the scale of observation: the effect of dispersal on beta-diversity was stronger during the first half of the experiment (approximately from week 3 to week 10) at the local community scale (Fig. 2d), while being stronger during the second half (from week 10 to week 15) at the metacommunity scale (Fig. 2e).

Individual species

The Mantel test revealed that predator differences were important for species composition both at local community and metacommunity scales. There was a significant effect

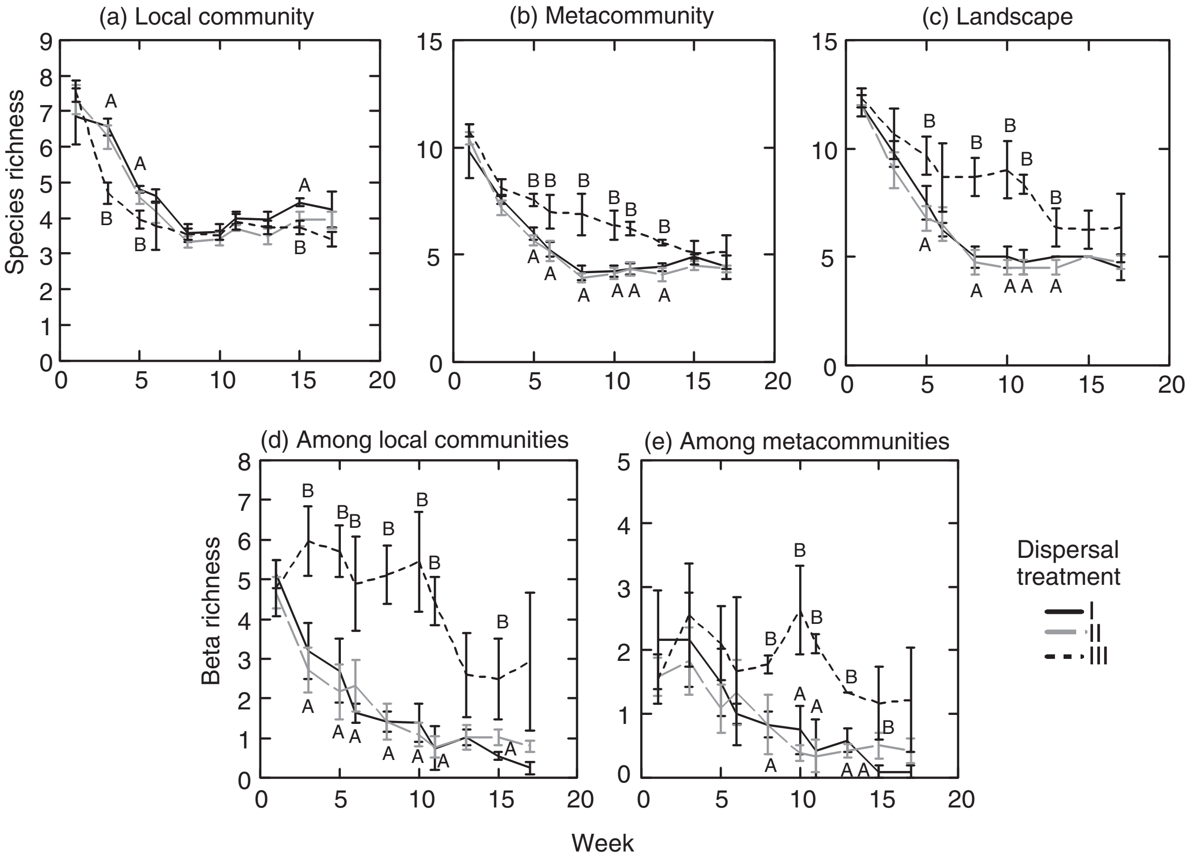

Figure 2 (a, b, c) Temporal changes in species richness observed at different scales of observation (mean ± SEM). (d, e) Temporal changes in beta-diversity, measured as richness at landscape scale minus mean richness at local community scale (d) or at metacommunity scale (e). Alphabet labels refer to significant differences among dispersal treatments at individual sampling dates.

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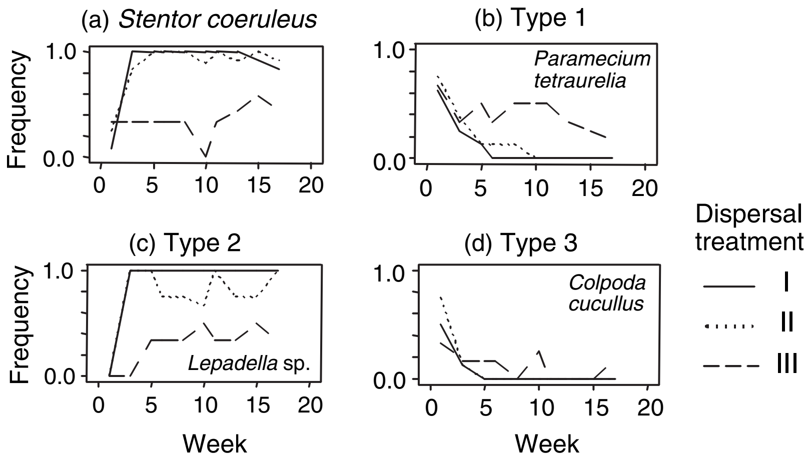

Figure 3 Temporal changes in the frequency of *Stentor* and representative species that each belong to type 1, 2, and 3 (see *Individual species* in Results). Frequency refers to the proportion of the local communities in which the species was recorded. The *Stentor* and type 2 species graphs show communities in which the focal species were initially absent. Type 1 and 3 species graphs are from communities where *Stentor* was initially absent, but focal species was initially present. See Supplementary Material for the results for other species.

associated with predation at week 6 (local community scale: $r = 0.433$, $P = 0.007$; metacommunity scale: $r = 0.581$, $P = 0.018$) and week 11 (local community scale: $r = 0.306$, $P = 0.024$; metacommunity scale: $r = 0.357$, $P = 0.050$), although this effect disappeared by week 17 (local community scale: $r = -0.072$, $P = 0.337$; metacommunity scale: $r = -0.136$, $P = 0.262$). The same trends were evident in a Mantel test that used the dissimilarity in *Stentor* abundance rather than the dissimilarity in all predators, indicating that the patterns were driven by *Stentor* rather than by the other predators, which rapidly went extinct in the presence of *Stentor*. Further, *Stentor* rapidly colonized unoccupied patches when permitted to disperse (Fig. 3a).

The results indicate that the other species can be categorized into three groups based on their response to dispersal treatments and to *Stentor* (see Supplementary Material). Type 1 species (*Chilomonas*, *Colpidium*, *Lacrymaria*, *Paramecium caudatum*, *P. tetraurelia* and *Uronema*) appeared to be affected negatively by dispersal and *Stentor* (Fig. 3b; Supplementary Material). All these species except *Uronema* were recorded more frequently and for a longer time in treatment III than in I and II and, within treatment III, in the local communities where *Stentor* was initially absent. *Uronema*'s frequency was also negatively affected by *Stentor*, although they recovered as *Stentor* abundance decreased over time. Type 2 species (*Lepadella*, *Rotaria*, and *Spirostomum*) appeared to be affected positively by dispersal (Fig. 3c; Supplementary Material). No clear effect of *Stentor* was observed on the frequency of these species. Type 3 species (*Colpoda cucullus*, *Colpoda inflata*, *Didinium* and *Tetrahymena*) quickly went extinct from most local communities by week 3 (Fig. 3d; Supplementary Material). Extinction patterns of these species did not seem to be affected by dispersal or *Stentor*.

DISCUSSION

In this hierarchically structured experimental landscape, dispersal had negative, positive and non-significant influences on species richness, depending on the successional stage and the scale of observation. At the local community scale, dispersal had a positive effect primarily during early stages of the experiment, although this effect quickly disappeared. By contrast, at the metacommunity and landscape scales, dispersal did not influence richness during early stages, but later showed a strong negative effect for a long period before richness eventually converged among dispersal treatments. Furthermore, dispersal negatively affected beta diversity between local communities primarily for the first half of the experiment, while affecting beta diversity between metacommunities only during the second half of the experiment. What mechanisms cause diversity patterns to depend so greatly on both time and space in this experimental landscape?

Mechanisms

Our data indicate that the varied responses of species to dispersal (Fig. 3, see also Supplementary Material) collectively caused diversity patterns to depend on the timing and scale of observation (Fig. 2). During the early stage of the experiment, the species that were affected positively by dispersal caused dispersal to increase local community diversity, while not affecting metacommunity or landscape diversity, because no variation in species composition initially existed among metacommunities or landscapes. However, as local species extinctions accumulated over time, the positive dispersal effect on local diversity was offset by the negative dispersal effect mediated by removal of local spatial refuges from negative species interactions, primarily with the generalist predator, *Stentor*. Hence, dispersal treatments converged in terms of local community diversity by week 6 (with the exception of week 15).

Although some of the local communities not connected by dispersal (landscape III) did not initially contain *Stentor* and thus were free from the negative effect of this species, most local communities in this landscape did contain *Stentor*. Thus, on average, local diversity of treatment III was not significantly different from that of treatment I or II, but a small number of communities that acted as spatial refuges from the local effect of *Stentor* in treatment III contributed to greater total richness maintained at the metacommunity and landscape scales. If *Stentor* acted as a keystone predator to maintain prey diversity (Paine 1966; Leibold 1996; Shurin & Allen 2001), the opposite pattern would have been observed, with metacommunity and landscape diversity being higher in treatment I and II than in III (e.g. Robinson & Edgemon 1989). This did not happen, because only one species [i.e. *Spirostomum*, which was probably invulnerable to *Stentor* (See Supplementary Material)] benefited from the presence of *Stentor*, while several other species were negatively affected by *Stentor*. The difference in the timing and scale at which the opposing effects of dispersal occurred (spread of species versus spatial refuge removal) is likely to be also responsible for the different timing in which dispersal affected beta diversity between local communities vs. between metacommunities.

In our experiment, dispersal among metacommunities did not significantly influence species diversity at any scale of observation (i.e. treatment I vs. II), in contrast to the strong effects of dispersal that occurred among local communities. This absence of an effect of among-metacommunity dispersal may also be the result of the strong *Stentor* effect. Our experimental design began with *Stentor* (and all other species in our species pool) introduced to all metacommunities regardless of dispersal treatments. Thus, all metacommunities had the same initial species composition, whereas local communities varied in initial composition. Therefore, dispersal had a minor effect compared with initial species composition in our experimental landscape.

A possible explanation of our observations can be found in hierarchy theory (e.g. Kotliar & Wiens 1990; Kolasa & Waltho 1998). The grain and extent (the smallest and largest scales at which organisms perceive environmental heterogeneity, respectively) of our experimental landscape likely vary depending on species (Kotliar & Wiens 1990). For our prey species, the grain is at or below the individual community, whereas the extent can be at any scale above this. The extent is likely at the metacommunity-level as there were no differences between landscapes I and II. *Stentor*, which appears to homogenize local communities, may perceive the grain at the landscape scale. *Stentor* has lower reproductive rate and larger habitat use, compared with the smaller prey species. The lower reproductive rate means that dispersal events may be frequent enough to prevent the decoupling of population dynamics. Mobility of this sort will shift patch perception to broader scales (Kotliar & Wiens 1990).

General implications

The strong impact of predation observed in this experiment is not meant to be a general prediction of how predation and dispersal will shape diversity at different spatial scales. Rather, our results indicate that the role of specific predators may need to be considered before any general processes can be understood about dispersal effects at multiple scales (e.g. McPeek 1998). For example, Robinson & Edgemon (1989) found a very different effect of predation on algal communities in a microcosm experiment similar to the present study. Their predator had a low impact on individual populations and promoted species richness by enhancing dispersal effect. One likely reason for the contrast between their results and ours is that their experiment took place over a single generation of the predator, whereas ours lasted for multiple generations of the predator. Obviously, the importance of predators to species diversity depends also on how general the predators are in consuming prey and how vulnerable the prey species are in avoiding predation. Our results may be especially applicable to islands and other insular habitats in which many prey species are highly vulnerable to generalist predators.

Regardless of the exact effects of predators, a broader implication of our results is that inferences regarding effects of dispersal on species diversity can be very different depending on the spatial scale of observation. For example, if we were examining a system where we were not able to discern the difference between the local community and the metacommunity, then we would have expected that treatments II and III (both without dispersal among metacommunities) to show similar patterns when viewed at the metacommunity and landscape scales. This was not the case, and begs the question of exactly what we mean by 'regional' processes when we are concerned with effects of dispersal on community structure (see also Loreau 2000). For a systematic understanding of dispersal effects, we need to correctly determine the grain and extent of the hierarchically structured environment, as suggested by hierarchy theory (e.g. Kotliar & Wiens 1990; Kolasa & Waltho 1998).

Our results also suggest that the rate of transient dynamics changes with dispersal and the scale of observation. Specifically, we identify three implications of our results in this respect. First, dispersal can make communities reach

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equilibrium faster at multiple scales. Second, the richness-promoting effect that isolation has on beta richness can occur later when observed at the among-metacommunity scale rather than at the among-local community scale. Third, the importance of spatial scale in understanding dispersal effects may be most clearly pronounced during non-equilibrial dynamics such as faunal relaxation (e.g. Robinson 1999).

Furthermore, our results provide new experimental evidence that connecting local communities can have negative consequences for species richness at several spatial scales. Dispersal is an important part of maintaining populations and species richness (Brown & Kodric-Brown 1977). However, other processes, particularly predation, may compromise the utility of dispersal (Kneitel & Miller 2003). The claim that there is conservation benefit in linking isolated habitats has been challenged (e.g. Simberloff & Cox 1987). The main concern is that linkage corridors may allow negative ecological interactions (e.g. disease, fire, invasion, predation) to spread among habitats. Our results show that while negative effects of predation on species diversity may not be realized at the local community level, they may be at larger scales. Predators may perceive spatial scale differently and serve to homogenize habitats when allowed to disperse.

Future directions

Laboratory microcosm experiments (Warren 1996a,b; Fukami & Morin 2003) will remain a powerful tool for initial empirical tests of the role of multiscale dispersal in various types of ecological landscapes. Our experiment can be thought of as simulating any patchy landscapes, especially those in which immigration dynamics depend on discontinuous dispersal (e.g. islands, old-fields, ponds, coral reefs). Further, our experiment simulates a succession initiated by large-scale disturbance affecting all communities in a landscape essentially to the same degree (e.g. succession after large-scale disturbance, such as a hurricane, drought, or flood) and with little variation in the time taken for different species to arrive at newly opened local sites [as assumed by Egler's (1954) initial floristic composition model of succession]. Other natural landscapes are subject to habitat destruction that operates more locally (e.g. gaps in forests, and ice scour in rocky intertidal shores). It will be important to examine these other types of landscape dynamics to determine the robustness of our results (Warren 1996b).

The amount of effort required for maintaining our system restricted us to using a limited number of dispersal treatments. We compared no dispersal with a relatively rapid dispersal. However, theory suggests that species diversity can show nonlinear responses to dispersal rate (Loreau & Mouquet 1999), which can be detected only when more than two dispersal rates are examined. Similarly, our dispersal treatment involved passive sampling (see also Warren 1996a,b) to show that hierarchical structuring by dispersal affects diversity even without ecological trade-offs. It will be interesting to use active dispersal (Holyoak & Lawler 1996) to examine the role of trade-offs (Horn & MacArthur 1972; Kneitel & Chase 2004) in hierarchical landscapes. Finally, habitat heterogeneity (in for example, resource availability) among local communities can enhance the effect of source-sink dynamics on species diversity (Forbes and Chase 2002), which should also be considered in future research in hierarchical landscapes.

Conclusion

Dispersal has been known to influence diversity through several mechanisms, including spatial refuge, source-sink, keystone predation and rescue effects, sometimes operating in opposing directions (Leibold *et al.* 2004). These varying effects of dispersal have puzzled ecologists because they make it difficult to systematically understand the role of dispersal in complex communities. The relative importance of these various mechanisms can depend seemingly idiosyncratically on details of biotic interactions (e.g. Shurin & Allen 2001). By directly manipulating dispersal at multiple scales, we have shown that, even given the same species pool and thus the same potential biotic interactions, the relative importance of the various mechanisms can change greatly over time and space in hierarchically structured landscapes. For this reason, we suggest that understanding species diversity requires explicit consideration of dispersal occurring at multiple scales rather than at one particular 'regional' scale.

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SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE750/ELE750sm.htm

Appendix S1 Patch occupancy graphs for each species used in the experiment.

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