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The effects of resource enrichment, dispersal, and predation on local and metacommunity structure

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Abstract Community structure is the observable outcome of numerous processes. We conducted a laboratory experiment using a microbial model system to disentangle effects of nutrient enrichment, dispersal, and predation on prey species richness and predator abundance at local and metacommunity scales. Prey species included: *Chilomonas* sp., *Colpidium striatum*, *Colpoda cucullus*, *Paramecium tetraurelia*, *P. caudatum*, *Philodina* sp., *Spirostomum* sp., *Tetrahymena thermophila*, and *Uronema* sp., and *Stentor coeruleus* was the predator used. We hypothesized that: (1) increased basal resources should maintain greater species richness and higher predator abundance; (2) dispersal should maintain greater species richness; and (3) predation should reduce species richness, especially in the high resource treatments relative to no-predator treatments. Our results support all three hypotheses. Further, we show that dispersal affects richness at the local community scale but not at the metacommunity scale. However, predation seems to have major effects at both the local and metacommunity scale. Overall, our results show that effects of resource enrichment, dispersal, and predation were mostly additive rather than interactive, indicating that it may be sometimes easier to understand their effects than generally thought due to complex interactive effects.

Keywords Dispersal · Metacommunity · Microcosm · Predation · Spatial scale

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Introduction

At the heart of the science of ecology is how multiple processes interact to produce extant patterns of species abundances, distributions, and diversity. Consequently, two unresolved issues in community ecology are: (1) how local and regional processes interact to produce patterns of species richness (e.g., Holt 1993; Holt et al. 1997; Loreau and Mouquet 1999; Shurin 2000; Amarasekare and Nisbet 2001; Shurin and Allen 2001; Cottenie et al. 2003; Kneitel and Miller 2003); and (2) how resource availability affects species diversity and interactions (e.g., Luckinbill 1974; Huston and DeAngelis 1994; Waide et al. 1999; Fukami and Morin 2003). We examine three fundamental community-structuring biotic processes that address these two unresolved issues: interspecific competition for resources, predation, and dispersal among local patches.

These three community-structuring processes have disparate histories, and therefore have separate theoretical underpinnings. First, competition has long been a central paradigm in ecology (e.g., Darwin 1859; Warming 1909; Gause 1934; Pianka 1966; MacArthur and Levins 1967; Tilman 1982; Chase and Leibold 2003). One influential modern version is a simple, but powerful concept: the idea that the competitor who can survive at the lowest resource level will likely outcompete co-existing species (i.e., R^*; Tilman 1982; Leibold 1996; Chase and Leibold 2003). In the current study, we use local communities that differ in resource concentrations as a surrogate of strength of competition.

Competition, therefore, limits community richness while the next disparate process, the immigration of individuals into local communities, can increase species richness by allowing species to find empty patches or resources and potentially escape dominant competitors (i.e., competition–colonization tradeoff; Holmes and Wilson 1998; Amareskare and Nisbet 2001; Mouquet and Loreau 2002; Levine and Rees 2002; Cadotte 2006a). In a metacommunity framework, immigration into local communities is dependent upon those leaving other communities. Metacommunity dispersal can reduce competition-caused extinctions in local communities (Cadotte 2006a, b), likely because extinction-prone populations are subsidized from larger, more secure populations (i.e., source–sink dynamics; Brown and Kodric-Brown 1977; Mouquet and Loreau 2002). The relative importance of these mechanisms (competition–colonization tradeoff vs source–sink dynamics) in a closed metacommunity, with no disturbance or external colonists, will depend upon stochastic extinctions or predation-caused extinctions.

The final disparate process, predation, is often thought to largely have a positive effect on the maintenance of local richness by reducing competition among species by reducing abundances, freeing resources or opening space (Paine 1966; Holt 1977; Holt and Lawton 1994; Leibold 1996; but see Addicott 1974; Cadotte and Fukami 2005). However, different species of predators are likely to show differential effects on different prey species (e.g., McPeek 1998; Chalcraft and Resetarits 2003; Jiang and Morin 2005), with generalist predators more likely to reduce local richness than specialist predators (Jiang and Morin 2005). Negative impacts from predation in metacommunities can reduce richness at larger scales by undoing dispersal's ability to increase richness (Kneitel and Miller 2003; Cadotte and Fukami 2005).

How these processes affect communities when they are manipulated simultaneously is not intuitive. Resource manipulation may be an efficacious surrogate for intracommunity competition if communities can be assumed to be at equilibrium (Tilman 1982; Waide et al. 1999). Kneitel and Miller (2003), building on the modeling work of Mouquet and Loreau (2002, 2003; Loreau et al. 2003), hypothesized that by decreasing competition (e.g., increasing resources) the effect of dispersal should be heightened, while increases in competition (lower resources) or predation rate should lessen the import of dispersal on community richness. They found that, in their inquiline communities in pitcher plants, resource manipulation had little impact on the effect of dispersal, while increasing predator abundance negated the dispersal effect.

However, enrichment can have other important interactions with predation, in the absence of dispersal. In simple tri-trophic systems, enriching three-tiered chains can result in increased abundances of predators (e.g., Rosenzweig 1973; Oksanen et al. 1981). Wootton and Power (1993) showed that increasing basal trophic-level productivity could result in higher abundances of predators. Following this, we would expect that enrichment of systems with predators should result in no change in the bacteriovore community structure with enrichment, since the extra biomass should be captured in the predatory trophic level (Jiang and Morin 2005).

Cadotte and Fukami (2005) found that, for protist metacommunities, dispersal among local communities only had a short-term enriching effect on local richness, while having long-term negative effects at larger spatial scales. In that experiment, they hypothesized that predator effects may have profoundly affected those results because the predator was able to move along with the prey in the dispersal treatments. More than this, a number of recent studies attempt to reconcile interactions among predation, competition, and dispersal (Loreau and Mouquet 1999; Shurin and Allen 2001; Kneitel and Miller 2003), and reveal that dispersal should offset losses due to competition, but that predation (especially from a dispersing generalist predator) should counter the dispersal benefit.

In this paper, we examine how predation, competition, and dispersal, all combine to structure local communities and generate richness patterns. We expect that: (1) in the absence of predators, local communities open to dispersal will maintain higher levels of diversity; while (2) increased resources will maintain greater species richness and will enhance the effect of dispersal; and that (3) the presence of a predator will diminish or negate the effects of dispersal, and have a greater impact on high resource communities as they attain higher abundances in these communities.

The experiment described in this paper uses a microcosm approach and addresses questions brought up in a previous experiment (Cadotte and Fukami 2005). In that experiment, predation was not explicitly manipulated, but it was apparent that richness patterns were differentially affected by dispersal and the presence of a generalist predator. Although microcosm experiments sacrifice natural context (Carpenter 1996), they offer many benefits (Drake et al. 1996; Cadotte et al. 2005). Microbial microcosms not only offer strict controls and replication, but also allow the researcher to observe multigenerational temporal dynamics, allowing them to be used in refining hypotheses and theories (Cadotte et al. 2005).

Materials and methods

We used three-community metacommunities, in which the local communities were 250-ml jars filled with 100 ml of nutrient solution. Within the metacommunities were three resource levels of varying concentrations of protozoa pellets and vitamins. The three local communities, each having a different resource level, constituted an intra-metacommunity treatment. There were two other metacommunity-level treatments: (1) the presence of a predatory species; and (2) dispersal among local communities within the metacommunity. These two sets of treatments resulted in four metacommunity combinations: presence of a predator and dispersal (PD), presence of a predator only (P), dispersal with no predator (D), and a control without dispersal or predation (C). All metacommunities were replicated five times, meaning that each combination of predation and dispersal were replicated five times for each of the three resource levels. The dispersal consisted of removing 0.6 ml from all three local communities, homogenizing and redistributing among the local communities. The dispersal treatments were performed every 3.5 days (i.e., every third and seventh day).

Each local community consisted of 100 ml of nutrient solution (80 ml of stock solution plus 20 ml from initial species additions), with the resource concentrations being one of the three levels used in the experiment: high, medium, or low. The high resource level consisted of 1.0 g l^{-1} of protozoa pellets and 0.1 g l^{-1} of vitamins, the medium resource level consisted of 0.1 g l^{-1} of protozoa pellets and 0.01 g l^{-1} of vitamins, and the low resource level consisted of 0.01 g l^{-1} of protozoa pellets and 0.001 g l^{-1} of vitamins.

Five days prior to the initialization of local communities, the stock solution was inoculated with four bacterial species (*Bacillus cereus, B. subtilis, Proteus vulgaris, Serratia marcescens*) from stock cultures, as well as with bacteria from filtered prey species stock cultures, in order to introduce bacterial species that would subsequently be introduced with the prey species. Three days before initialization, microflagellates were introduced.

A total of 11 protozoan and rotifer species were used in this experiment: 1 generalist predator, *Stentor coeruleus*, and 10 prey species (Table 1). The same local community species assemblages were used in each treatment and each replicate. The average generation time for the organisms involved is about a day. This experiment lasted 8 weeks, representing about 50–60 generations of the organisms involved.

Sampling

Once a week, 6 ml of community medium was removed and replaced with fresh medium of the concentration corresponding to the resource level from which it was taken. On sampling dates, the excised 6 ml was used as the source for the sample. Our sampling procedure consisted of individual-based full counts. The full counts were performed five times, in weeks 1, 2, 4, 6, and 8. From the 6-ml aliquots, we counted all individuals of each species from a 0.2-ml subsample. If species densities were too high to be accurately counted, we added 2 ml of sterile solution and again counted all the individuals in a 0.2-ml subsample of the dilution. Numbers of individuals were calculated per milliliter.

Table 1 The 11 protozoan and rotifer species, plus the basal trophic species used in this experiment

Species	Trophic level
Stentor coeruleus	Predator
Chilomonas sp.	Prey (bacteriovore)
Colpidium striatum	Prey (bacteriovore)
Colpoda cucullus	Prey (bacteriovore)
Colpoda inflata	Prey (bacteriovore)
Paramecium caudatum	Prey (bacteriovore)
Paramecium tetraurelia	Prey (bacteriovore)
Philodina sp.	Prey (bacteriovore, microflagellates)
Spirostomum sp.	Prey (bacteriovore, microflagellates)
Tetrahymena thermophila	Prey (bacteriovore)
Uronema sp.	Prey (bacteriovore)
Bacillus cereus	Basal (bacteria)
Bacillus subtilis	Basal (bacteria)
Proteus vulgaris	Basal (bacteria)
Serratia marcescens	Basal (bacteria)
Microflagellates	Intermediate

Data analyses

Our data consisted of observations for the four metacommunity treatments (predation and dispersal) and the three intra-metacommunity treatments (resource level) across a time series. Our primary data were counts (species richness), and so we used loglinear models for analysis of this data. For local richness, we modeled predator (*Stentor*) presence/absence, dispersal presence/absence, resource level, time (week number), and all two-way interactions. We also combined the three interacting local communities to find metacommunity species richness, by recording species presence at the metacommunity scale (i.e., present in at least one local community). We analyzed all the same variables and two-way interactions, except for resource level, in a loglinear model. We also examined class comparisons within each independent variable. We report the class effect on the model (β), as well as the percent effect ($-e^{\beta}$) on species richness. We also analyzed Simpson's diversity index (not shown) and results largely confirmed the results based on the above analysis.

There was a potential confounding influence in that resource dynamics will change in the treatments with dispersal. If the dispersal effect on nutrient level was great enough to affected species richness, then the dispersal–resource–time three-way interaction term in the loglinear model should be significant, and would merit further discussion or analysis.

We used repeated measures ANOVA to determine if dispersal and resource level had significant effects on the abundance of *Stentor*. An assumption for the repeated measures *F*-test is that the variance–covariance matrix has compound symmetry. When there is departure from compound symmetry, corrections, which modify degrees of freedom, have been proposed by Huynh-Feldt and Greenhouse-Geisser. We used these corrections in determining *P* values. All statistics were done using SAS v.9.1 (SAS Institute).

Results

Intra-community patterns

At the local scale, all the main effects significantly affected richness (Tables 2, 3). Local communities

Table 2 Results of the loglinear model, modeling main effects and their two-way interactions on local and regional species richness

Source	*df*	X^2	*P*
Local richness			
Predator	1	40.77	**<0.0001**
Dispersal	1	7.10	**0.0077**
Resource	2	90.85	**<0.0001**
Week	4	101.75	**<0.0001**
Predator × dispersal	1	0.01	0.9415
Predator × resource	2	0.69	0.7086
Dispersal × resource	2	4.2	0.1222
Predator × week	4	22.17	**0.0002**
Dispersal × week	4	2.52	0.6411
Resource × week	8	3.60	0.8614
Regional richness			
Predator	1	32.59	**<0.0001**
Dispersal	1	0.09	0.7629
Week	4	62.99	**<0.0001**
Predator × dispersal	1	0.10	0.7493
Predator × week	4	18.60	**0.0009**
Dispersal × week	4	0.92	0.9220

df is the degrees of freedom and X^2 is the Chi-square statistic

Bold *P*-values are significant at $P=0.1$

Table 3 Results of the loglinear model, showing within class effects on local and regional species richness

Variable	Condition	Beta	% effect	*df*	X^2	*P*
Local richness						
Predator	Absent vs present	0.4087	50.5↑	1	3.36	**0.0669**
Dispersal	Absent vs present	−0.4523	36.4↓	1	3.94	**0.0472**
Resource	High vs low	0.6261	87.0↑	1	5.74	**0.0166**
	Medium vs low	0.3532	42.4↑	1	1.62	0.2037
Week	Week 1 vs equilibrium	0.9927	169.8↑	1	13.07	**0.0003**
	Week 2 vs equilibrium	0.7025	101.9↑	1	6.22	**0.0126**
	Week 4 vs equilibrium	0.3586	43.1↑	1	1.48	0.2244
	Week 6 vs equilibrium	−0.1524	14.1↓	1	0.21	0.6462
Regional richness						
Predator	Absent vs present	0.7584	113.5↑	1	7.06	**0.0079**
Week	Week 1 vs equilibrium	1.3540	287.3↑	1	21.29	**<0.0001**
	Week 2 vs equilibrium	1.0888	197.1↑	1	13.10	**0.0003**
	Week 4 vs equilibrium	0.3641	43.9↑	1	1.17	0.2790
	Week 6 vs equilibrium	0.2103	23.4↑	1	0.36	0.5465

Beta is from the loglinear model, showing the effect of moving from one class state to another (e.g., from predator present to absent). % effect is the percent change in richness in the model as a result of the state change

df is the degrees of freedom and X^2 is the Chi-square statistic

Bold *P*-values are significant at $P=0.1$

without *Stentor* averaged 50.5% more species than those with *Stentor*. Similarly, without dispersal, local communities showed a reduction of 36.4% in species richness compared to those with dispersal. Richness also declined with lower resources and over time (Tables 2, 3, Fig. 1).

One interaction term (predator × week) was significant (Table 2). This corresponded to different temporal trajectories dependent upon the presence of *Stentor*. In the presence of *Stentor*, richness showed an exponential decline over time, while in the absence of *Stentor*, richness showed a unimodal curve (Fig. 1).

We also tested the three-way interaction between dispersal, resource level, and time. We found that this interaction had no significant effect on species richness ($\chi^2=2.95$, $P=0.9373$), which leads us to conclude that resource change with dispersal had no effect on our results.

Metacommunity patterns

When we pooled all three local communities together and examined patterns at the metacommunity, the negative effects of predation were much more obvious (Fig. 2). At this scale, the presence of dispersal had no effect on richness ($P=0.7629$), while the presence of *Stentor*, time, and the *Stentor*–time interaction all significantly affected richness (Table 2). Without *Stentor*, metacommunity richness was on average 113.5% higher than those without *Stentor* (Table 3).

Species dynamics

Several species (*Chilomonas*, *Colpidium*, *Colpoda inflata*, *Paramecium caudatum*, and *Tetrahymena thermophila*) quickly went extinct or had idiosyncratic dynamics. These idiosyncratic dynamics mean that the species in question would appear as a single or as very few samples at different sampling dates and not in the same replicate. The rest of the species revealed more tractable dynamics. Three species (*Colpoda cucullus*, *Paramecium tetraurelia* and *Uronema*) appeared to be adversely affected by the presence of the predator, while two species (*Philodina* and *Spirosomum*) were largely unaffected by the predator.

The predator, *Stentor coeruleus*, was unaffected by communities being open to dispersal ($F_{1,96}=0.08$, $P=0.7745$), but was significantly affected by community resource level ($F_{2,96}=29.45$, $P<0.0001$; Fig. 3), with high resource patches maintaining significantly higher *Stentor* abundances after the first sampling date (Tukey's post hoc test, $P<0.05$ for sampling weeks 2–8). Stentor abundance also declined over time ($F_{4,96}=22.86$, $P<0.0001$). Further, resource level and time showed a significant interaction ($F_{8,96}=23.21$, $P<0.0001$), where high resource communities showed unimodal or logistic increases (with possible oscillations), while medium and low resource levels showed linear declines in the *Stentor* populations (Fig. 3).

Discussion

We were interested in disentangling the effects of predation and dispersal, and developed hypotheses as to the

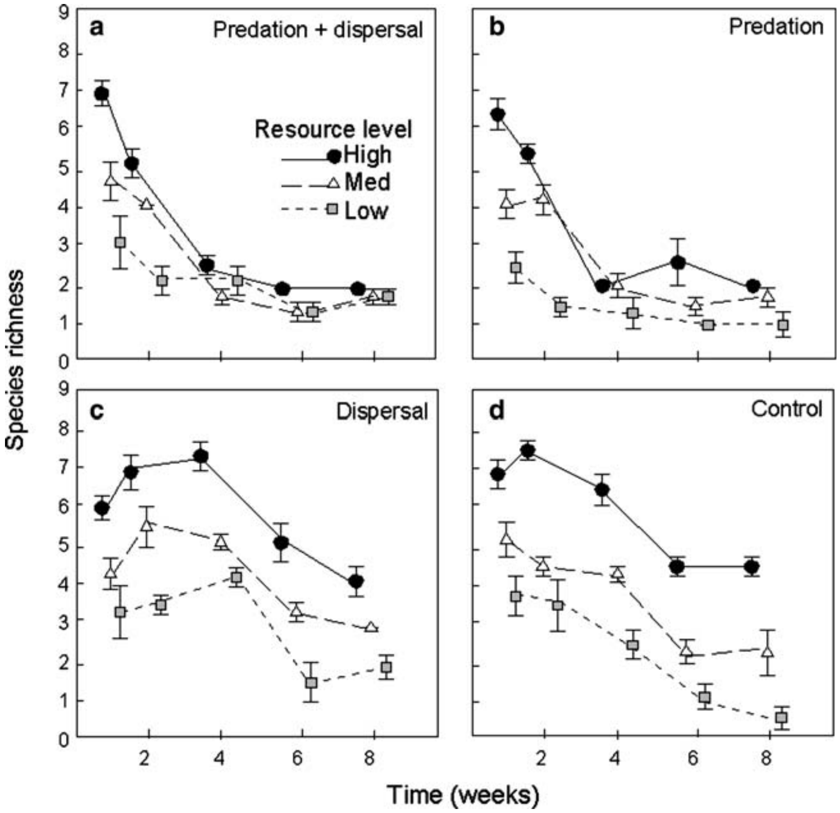

Fig. 1 Local prey community species richness during the 8-week study in each combination of predation/dispersal treatment (**a** *Predation + dispersal*, **b** *Predation*, **c** *Dispersal*, **d** *Control*) at high, medium, and low resource levels (means±SE, $n = 5$). Prey species include: *Chilomonas* sp., *Colpidium striatum*, *Colpoda cucullus*, *Colpoda inflata*, *Paramecium tetraurelia*, *P. caudatum*, *Philodina* sp., *Spirostomum* sp., *Tetrahymena thermophila*, and *Uronema* sp

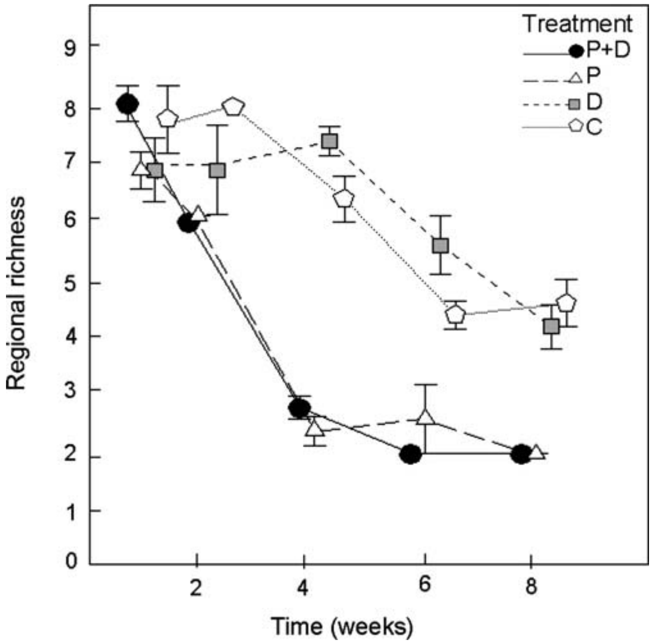

Fig. 2 Regional (metacommunity) species richness during the 8-week study for predation and dispersal ($P + D$), predation (P), dispersal (D), control (C), (mean±SE, $n = 5$)

directions of their effects from the literature (Mouquet and Loreau 2002, 2003; Kneitel and Miller 2003) and in response to the findings of a previous experiment (Cadotte and Fukami 2005). We hypothesized that predation would reduce or negate the richness by increasing effect of dispersal. Furthermore, higher basal resource concentration may enhance the effect of dispersal. Therefore, if we did see any effect of dispersal in the treatments with predation, it should be at high resource concentrations. Our results revealed that our predator, *Stentor coeruleus*, reduced richness to two species, regardless of resource concentration and dispersal treatment. This effect is very apparent at the metacommunity level (Fig. 2). Therefore, predation appears to be an important community structuring mechanism regardless of spatial scale (see also Cadotte and Fukami 2005). Different predators have differential effects on prey species richness and abundance (McPeek 1998; Steiner 2001). *Stentor* is an efficacious generalist predator (Cadotte and Fukami 2005; Jiang and Morin 2005). Our results reveal some of the ecological consequences of a generalist predator.

At the local scale, dispersal had beneficial effects on richness at intermediate timescales. Even though there appeared to be some benefit of dispersal in the presence of our predator (see also Holyoak and Lawler 1996a, b), predation dramatically reduced richness compared to the no-dispersal treatment. However, at the metacommunity scale, dispersal had little or no effect on richness (see Cadotte 2006a for an examination of the pervasiveness of this pattern in the ecological literature). Therefore, we view dispersal as an important local rather than regional structuring mechanism. The results from this study explain the patterns observed in Cadotte and Fukami (2005). In that study, dispersal appeared to have no effect at the local community, but appeared to maintain lower

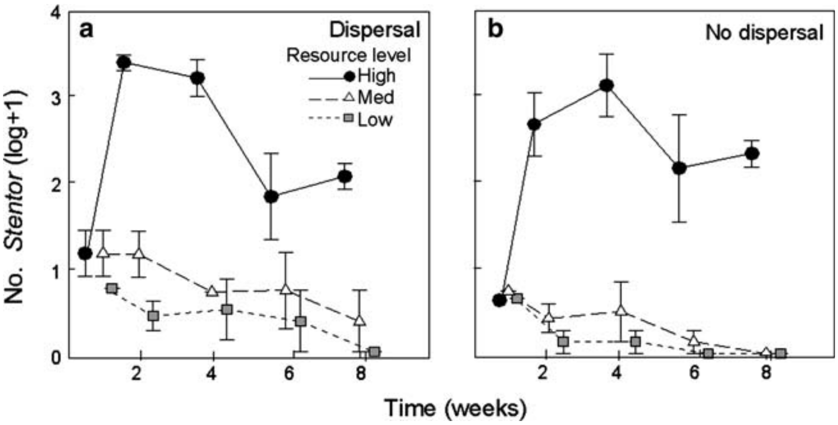

Fig. 3 The number of *Stentor coeruleus* (log+1) at high, medium and low resource levels, (mean±SE, $n=5$) with **a** dispersal and **b** no dispersal

diversity in the metacommunity. They realized that, because the strongest predator, *Stentor coeruleus*, was not found in every local community, dispersal effects were confounded with predator effects. Our current results reveal that the pattern of lower regional diversity found in Cadotte and Fukami (2005) are likely the result of the regional structuring effect of *Stentor*, similar to what is shown in Fig. 2. Similarly, Warren (1996) found that dispersal rate had a minor effect on community structure, but was significant for individual species abundances (see also Holt et al. 2002). Warren's (1996) experimental design also included a generalist top predator (*Amoeba proteus*) which may have been, similar to our findings and that of Kneitel and Miller (2003), an important mechanism structuring communities and reducing the effect of dispersal. Jiang and Morin (2005) examined how specialist and generalist predators structure local communities. They found that communities with the specialist predator exhibited bottom-up control of the prey community, while with the generalist, top-down processes were in control.

Shurin and Allen (2001) showed that, even though dispersal can promote coexistence between competing species, inclusion of an effective, dispersing predator could potentially reduce local diversity. Their model also shows that predation, even though it reduces local diversity, may enable further invasions and maintain higher regional diversity. Our results show that the presence of a predator strongly diminishes species coexistence at both the local and metacommunity levels. Although in a more complex experimental mesocosm, Shurin (2001) found that dispersal provided a rescue effect for zooplankton when, without dispersal, predation drove many to extinction. Shurin (2001) also showed that the presence of predators did facilitate subsequent invasions by other zooplankton. It is difficult to say how our findings would hold, given an open species pool.

Our view of predation is like that of Shurin and Allen (2001), where the predator is a member of the community and therefore influenced by dispersal. In a sense our design is not truly factorial, because predator dynamics can change with dispersal. This reality may limit our understanding of how dispersal and predation structure prey communities as independent processes. However, we feel that the current results are pertinent to factors structuring communities and to conservation issues concerning fragmentation and habitat connectivity.

Several authors have noted that predator abundances are often positively affected by resource enrichment, perhaps more than other trophic levels below the predator (e.g., Leibold 1996; Bohannan and Lenski 1997, 1999; Kaunzinger and Morin 1998; Jiang and Morin 2005). Enrichment is thought to have a number of other consequences for community structure, beyond relaxing competition. Enrichment can destabilize predator–prey interactions, increasing the probability that one or both species go extinct (Luckinbill 1974). Conversely, enrichment is thought to support longer food chains, with lower probability of top predator extinction (e.g., Leibold 1996). Our results show that, over the course of the experiment, predator population abundances were enhanced by resource enrichment. Jiang and Morin (2005) showed that increases in generalist predator abundance with increasing nutrients are a logical consequence of increased reproduction in prey populations. However, they point out that specialists are unlikely to similarly benefit because of shifts in prey composition or size.

Conclusions

Dispersal and predation are known to affect species diversity, sometimes in interactive or negating ways (Knietel and Miller 2003; Leibold et al. 2004). These effects can be difficult to understand as universal processes. However, by examining these effects at different spatial and temporal scales, it becomes possible to dissect the relative effects of predation, competition, and dispersal. We show that: (1) increased resources supported higher prey diversity; (2) increased resources supported higher predator abundances; (3) dispersal increased local richness both in the presence and absence of the predator, but the negative impact of predation on richness was much stronger than the positive dispersal effect; (4) dispersal enhances local richness, and not metacommunity richness; and (5) predation structures communities at multiple spatial scales. These results show that although competition, predation and dispersal have differing effects on the maintenance of species richness, they actually may not have interactive effects, rather they appear additive, at least when examining dispersal as a binary factor (as opposed to a continually varying factor, e.g., Mouquet and Loreau 2002). In such cases, it may be sometimes easier to understand their effects than generally thought due to complex interactive effects.

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References

Addicott JF (1974) Predation and prey community structure: an experimental study of the effect of mosquito larvae on the protozoan communities of pitcher plants. Ecology 55:475–492

Amarasekare P, Nisbet RM (2001) Spatial heterogeneity, source–sink dynamics, and the local coexistence of competing species. Am Nat 158:572–584

Bohannan BJ, Lenski RE (1997) Effect of resource enrichment on a chemostat community of bacteria and bacteriophage. Ecology 78:2303–2315

Bohannan BJ, Lenski RE (1999) Effect of prey heterogeneity on the response of a model food chain to resource enrichment. Am Nat 153:73–82

Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449

Cadotte MW (2006a) Dispersal and species diversity: a meta-analysis. Am Nat (in press)

Cadotte MW (2006b) Metacommunity influences on community richness at multiple spatial scales: a microcosm experiment. Ecology (in press)

Cadotte MW, Drake JA, Fukami T (2005) Constructing nature: laboratory models as necessary tools for investigating complex ecological communities. Adv Ecol Res 37:333–353

Cadotte MW, Fukami T (2005) Dispersal, spatial scale and species diversity in a hierarchically structured experimental landscape. Ecol Lett 8:548–557

Carpenter SR (1996) Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77:677–680

Chalcraft DR, Resetarits WJ (2003) Predator identity and ecological impacts: functional redundancy or functional diversity? Ecology 84:2407–2418

Chase JM, Leibold MA (2003) Ecological niches: linking classical and contemporary approaches. University of Chicago Press

Cottenie K, Michels E, Nuytten N, De Meester L (2003) Zooplankton metacommunity structure: regional vs local processes in highly interconnected ponds. Ecology 84:991–1000

Darwin C (1859) The origin of the species. Murray, London

Drake JA, Huxel GR, Hewitt C (1996) Microcosms as models for generating and testing community theory. Ecology 77:670–677

Fukami T, Morin PJ (2003) Productivity–diversity relationships depend on the history of community assembly. Nature 424:423–426

Gause GF (1934) The struggle for existence. Williams and Wilkins. Baltimore

Holmes EE, Wilson HB (1998) Running from trouble: long distance dispersal and the competitive coexistence of inferior species. Am Nat 151:578–586

Holt AR, Warren PH, Gaston KJ (2002) The importance of biotic interactions in abundance–occupancy relationships. J Anim Ecol 71:846–854

Holt RD (1977) Predation, apparent competition, and the structure of prey communities. Theoret Popul Biol 12:197–229

Holt RD (1993) Ecology at the mesoscale: the influence of regional processes on local communities. In: Ricklefs R, Schluter D (eds) Species diversity in ecological communities, University of Chicago Press, Chicago, pp 77–88

Holt RD, Lawton JH (1994) The ecological consequences of shared natural enemies. Annu Rev Ecol Syst 25:495–520

Holt RD, Lawton JH, Gaston KJ, Blackburn TM (1997) On the relationship between range size and local abundance: back to basics. Oikos 78:183–190

Holyoak M, Lawler SP (1996a) Persistence of an extinction-prone predator–prey interaction through metapopulation dynamics. Ecology 77:1867–1879

Holyoak M, Lawler SP (1996b) The role of dispersal in predator–prey metapopulation dynamics. J Anim Ecol 65:640–652

Huston MA, DeAngelis DL (1994) Competition and coexistence: the effects of resource transport and supply rates. Am Nat 144:954–977

Jiang L, Morin PJ (2005) Predator diet breadth influences the relative importance of bottom-up and top-down control of prey biomass and diversity. Am Nat 165:350–363

Kaunzinger CMK, Morin PJ (1998) Productivity controls food-chain properties in microbial communities. Nature 395:495–497

Kneitel JM, Miller TE (2003) Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inequilines. Am Nat 162:165–171

Leibold MA (1996) A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. Am Nat 147:784–812

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase J, Hoopes M, Holt R, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecology Lett 7:601–613

Levine JM, Rees M (2002) Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. Am Nat 160:452–467

Loreau M, Mouquet N (1999) Immigration and the maintenance of local species diversity. Am Nat 154:427–440

Loreau M, Mouquet N, Gonzalez A (2003) Biodiversity as spatial insurance in heterogeneous landscapes. Proc Natl Acad Sci USA 100:12765–12770

Luckinbill LS (1974) The effects of space and enrichment on a predator–prey system. Ecology 55:1142–1147

MacArthur RH, Levins R (1967) The limiting similarity, convergence and divergence of coexisting species. Am Nat 101:377–385

McPeek MA (1998) The consequences of changing the top predator in a food web: a comparative experimental approach. Ecol Monogr 68:1–23

Mouquet N, Loreau M (2002) Coexistence in metacommunities: the regional similarity hypothesis. Am Nat 159:420–426

Mouquet N, Loreau M (2003) Community patters in source–sink metacommunities. Am Nat 162:544–557

Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. Am Nat 118:240–261

Paine RT (1966) Food web complexity and species diversity. Am Nat 100:65–75

Pianka ER (1966) Latitudinal gradients in species diversity: a review of concepts. Am Nat 100:33–46

Rosenzweig ML (1973) Exploitation in three trophic levels. Am Nat 107:275–294

Shurin JB (2000) Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. Ecology 81:3074–3086

Shurin JB (2001) Interactive effects of predation and dispersal on zooplankton communities. Ecology 82:3404–3416

Shurin JB, Allen EG (2001) Effects of competition, predation, and dispersal on species richness at local and regional levels. Am Nat 158:624–637

Steiner CF (2001) The effects of prey heterogeneity and consumer identity on the limitation of trophic-level biomass. Ecology 82:2495–2506

Tilman D (1982) Resource competition and community structure. Princeton University Press

Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, Parmenter R (1999) The relationship between productivity and species richness. Annu Rev Ecol Syst 30:257–300

Warming E (1909) Oecology of plants: an introduction to the study of plant communities. Clarendon Press, Oxford

Warren PH (1996) The effects of between-habitat dispersal rate on protist communities and metacommunities in microcosms at two spatial scale. Oecologia 105:132–140

Wootton JT, Power ME (1993) Productivity, consumers, and the structure of a river food chain. Proc Natl Acad Sci USA 90:1384–1387