

DISPERSAL LIMITATION, INVASION RESISTANCE, AND THE STRUCTURE OF POND ZOOPLANKTON COMMUNITIES

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Abstract. For a species to colonize a site it must both arrive there by dispersal from another site and maintain positive population growth in the local environment. I experimentally tested the role of dispersal limitation in structuring the zooplankton communities of fishless ponds in southwestern Michigan. An average of 12.9 new species of rotifers and crustaceans from the region were introduced at the beginning of the experiment into the intact resident communities of seven ponds in large in situ enclosures (the invasion treatment). Introduced species were found at least once over three months in six of the seven ponds, and one species consistently colonized all three replicate enclosures in three of the ponds. However, the success rate of the introductions was low as >91% of the species introduced immediately became extinct. In addition, introduced species remained rare throughout the experiment in every pond, comprising only 0–2.5% of total zooplankton community biomass. No effects of the invasion treatment were detected on total zooplankton diversity or biomass, on the biomass of native species, or on chlorophyll *a* concentration, suggesting that relaxing dispersal limitation for the regional pool had minimal effects on local community structure. Both the biomass of exotic species and the proportion of species introduced that successfully colonized the invasion treatment were negatively correlated with native species diversity. These patterns support the hypothesis that diversity confers resistance to invasion. The results of the invasion treatment indicated a minor role for dispersal limitation in structuring pond zooplankton communities.

To test the role of interactions with resident species in excluding potential invaders, a second experiment was performed in four different ponds the following year. In addition to the control and invasion treatment, a second treatment (the resistance treatment) was imposed where the abundance of native species was reduced by filtering before the introduction of invaders. The goal of this treatment was to weaken interactions between resident species and invaders while maintaining the abiotic environment intact. Among the four ponds, 3.8 times more exotic species were found in the resistance treatment than in the invasion treatment, and their total biomass was 16.4 times greater. The contrast between the invasion and resistance treatments indicated an important role for species interactions in repelling invaders. The two experiments showed that zooplankton communities were nearly saturated with species and that biotic interactions excluded many potential invaders.

Key words: *cladocerans; colonization; copepods; dispersal; exotic species; experimental introduction; ponds; species interactions; species invasion; rotifers; zooplankton.*

INTRODUCTION

The processes that structure ecological communities fall under one of two broad categories. Local processes are driven by aspects of the physical and biological environment that affect the persistence of populations within relatively small, homogeneous areas (hereafter called local sites or patches). Regional processes include dispersal among sites and extinction of local populations in a heterogeneous environment (MacArthur and Wilson 1967, Gilpin and Hanski 1991). The relative importance of local and regional processes in generating differences in diversity and composition among

sites depends on whether species are most often excluded from sites by local (biotic or abiotic) conditions (Diamond 1975, Case 1990, Drake 1991, Law and Morton 1996) or dispersal limitation (Sale 1977, Hubbell and Foster 1986, Roughgarden et al. 1988, Cornell and Lawton 1992, Tilman 1994, 1997, Caley and Schluter 1997). If dispersal rates greatly exceed local extinction probabilities for many species, then sites will contain nearly all of the species in the region capable of invading. In this case, local processes will dominate in shaping species diversity and composition within patches. Alternatively, if dispersal events are rare, then species will often be absent from suitable local sites and community structure is under strong regional control. In this case, local species composition depends on a site's history of colonization and local processes may play a minor role (Ricklefs 1987, Cornell and Lawton 1992, Cornell and Karlson 1997).

One approach to estimating the roles of local and

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TABLE 1. Hypotheses and predictions tested in this study.

Hypotheses	Predictions
1. Species of zooplankton are absent from ponds due to dispersal limitation.	Species will colonize when introduced in the invasion treatment.
2. Dispersal limits the diversity and biomass of zooplankton communities.	Zooplankton diversity and biomass will be greater in the invasion treatment than in the control.
3. Diverse communities are more resistant to invasion than species-poor communities (Elton 1958).	The effects of the invasion treatments will decline with increasing diversity of native zooplankton communities among ponds.
4. Interactions with native species exclude potentially invasive species.	Species excluded in the invasion treatment will invade in the resistance treatment.

regional processes in structuring communities is to examine the shape of the relationship between local and regional species richness among regions. This method is based on the prediction that, if local processes limit the number of species capable of coexisting within a site, then local species richness will approach an upper asymptote with increasing regional richness (Terborgh and Faaborg 1980, Cornell and Lawton 1992). Alternatively, if local richness increases continuously with increasing richness of the regional pool, then communities may be unsaturated or under strong regional control. Recent reviews of the literature on patterns of local and regional richness have concluded that linear, positive functions are common among many diverse groups of organisms (Cornell and Karlson 1997, Lawton 1999, Srivastava 1999). Many studies have taken linear patterns of local and regional richness to indicate that dispersal strongly limits local diversity and that species interactions and other local processes exert weak control (Ricklefs 1987, Cornell and Karlson 1997, Lawton 1999, Srivastava 1999).

The interpretation of these patterns is not straightforward, however, as mechanisms other than dispersal limitation may influence the shape of the relationship between local and regional diversity. For instance, disturbance can forestall competitive exclusion, leading to positive, linear patterns of local and regional richness even when dispersal is rapid and widespread (Caswell and Cohen 1993). In addition, the appropriate scale at which to define the local site is often unclear (Cornell and Lawton 1992, Caley and Schluter 1997, Westoby 1998). Environmental heterogeneity at scales smaller than the presumed local site can lead to spatial segregation among species and the apparent coexistence of species that do not interact with one another (Cornell and Lawton 1992, Westoby 1998). The shape of the pattern of local with respect to regional richness also depends on the choice of the regional scale (Angermeier and Winston 1998, Srivastava 1999, but see Shurin et al. 2000 for a scale-independent test with zooplankton). Finally, variation in aspects of the local environment among regions can influence the relationship between local and regional species richness (Huston 1999). Experimental species introductions are

therefore quite valuable for measuring the extent of dispersal limitation in natural communities, but are rarely performed because they are not feasible in most systems (but see Levins and Heatwole 1973, Tilman 1997).

I tested the roles of dispersal and biotic resistance to invasion in shaping the crustacean and rotifer zooplankton communities of fishless ponds in southwestern Michigan in two comparative experiments. The first experiment consisted of a control and one treatment (the invasion treatment), each replicated in field enclosures in seven ponds. In the invasion treatment, I introduced a diverse mixture of species from the region into intact local communities. The hypotheses addressed by the invasion treatment are listed in Table 1. The first is that some species of zooplankton are excluded from ponds by limited dispersal. In this case, I expected that relaxing dispersal limitation through experimental introductions would result in colonization of ponds by species that were previously absent. The number of successful invasions observed is a measure of the importance of dispersal in constraining species distributions among ponds.

The second hypothesis is that relaxing dispersal limitation would enhance local zooplankton diversity and biomass (Table 1). The consequences of dispersal limitation for local community structure depend on the processes that determine the diversity and abundance of species within sites. If dispersal limits local diversity, then productivity or standing biomass may also be below their intrinsic maximum potentials set by local constraints. In this case, experimentally relaxing dispersal limitation by species introductions may result in increased local diversity and community biomass (Tilman 1997). Alternatively, fugitive species may coexist regionally with better competitors by being superior colonizers of local sites (Levins and Culver 1971, Diamond 1975, Tilman 1994). In this case, introduced species from the regional pool may displace inferior competitors from sites and have positive, negative, or no effects on local diversity. If introduced species exclude residents through greater rates of resource use, then community biomass may also be enhanced by their introduction. This mechanism for re-

gional coexistence depends on an interspecific trade-off between the ability to compete for resources and to disperse (Levins and Culver 1971, Tilman 1994). Because there is no reason to suspect that such a trade-off exists in zooplankton, I predicted that zooplankton diversity and biomass would be greater in the invasion treatment than in the control. The impact of experimentally introduced species on target communities is a measure of the importance of dispersal limitation in generating local community structure.

The third hypothesis (Table 1) was that ponds with more diverse resident communities would be less susceptible to invasion than ponds with fewer native species (Elton 1958, Case 1990, Tilman 1997). There are two mechanisms by which more diverse communities are expected to experience fewer invasions than less diverse communities. The first is a sampling artifact that the regional pool contains fewer potential invaders in sites where more species are already present (MacArthur and Wilson 1967). The second is that more diverse communities may utilize resources more completely or efficiently so that less niche space is available for new species to occupy (Elton 1958, Case 1990, Robinson et al. 1995, Tilman 1997). The second mechanism predicts that both the probability of successful invasion by potential colonists and the abundance of exotic species once established will decline with increasing diversity of resident species. I tested these predictions by examining patterns in the effect size of the invasion treatment among ponds. That is, I asked whether the probability of success of species introductions or biomass of exotic species declined with increasing diversity of resident species.

The fourth hypothesis (Table 1) was that species interactions play a role in excluding invaders from zooplankton communities. To test this hypothesis, a second experiment was performed in which the control and invasion treatment were repeated in four additional ponds along with a second treatment (the resistance treatment). The goal of the resistance treatment was to maintain the abiotic environment of the ponds intact while weakening interactions between resident species and invaders. This was accomplished by filtering water in the enclosures through a plankton net to reduce the abundance of native zooplankton. The difference in the success rate and abundance of invasive species between the invasion and resistance treatments indicates the importance of species interactions in generating resistance to invasion and constraining community membership. The three hypotheses addressed by the invasion treatment were also tested in the second experiment.

Another objective of this study was to compare the results of the experimental test for the importance of dispersal limitation and local interactions in zooplankton with a widely used observational test. A companion paper (Shurin et al. 2000) describes an investigation of the global pattern of local and regional species richness in crustacean zooplankton. The observational study

TABLE 2. Pretreatment characteristics of the ponds used in the two experiments.

Pond	Surface area (m ²)	Resident richness	Fisher's alpha
Experiment 1			
A) Bird sanctuary 1	12072	21 (9, 12)	2.41
B) Pond Lab	1257	18 (4, 14)	1.21
C) L.A. 14	570	22 (6, 16)	1.61
D) L.A. 11	439	20 (6, 14)	2.35
E) L.A. 3	7107	19 (6, 13)	1.76
F) Entomology†	3960	17 (6, 11)	1.70
G) L.A. 16	942	16 (4, 12)	1.18
Experiment 2			
H) Bird sanctuary 2	300	22 (16, 6)	2.47
I) Shaw	4208	20 (10, 10)	1.74
J) Upton	4337	22 (14, 8)	1.94
K) L.A. 12	260	14 (10, 4)	0.79

Notes: Ponds identified with "L.A." are at the Lux Arbor Reserve. Species richness is the cumulative number of species identified in all the pretreatment bag and pond samples. Numbers in parentheses are (crustaceans, rotifers). Diversity (Fisher's alpha) is the mean of all pretreatment pond and bag samples excluding the resistance treatment.

† The experiment lasted only 33 d in this pond due to disturbance by ducks.

found that local crustacean richness was a continuous, positive function of the richness of the regional species pool. Such patterns have often been interpreted to indicate that communities are under strong regional control and that local processes exert weak influence, relative to dispersal, in structuring local communities (see Cornell and Lawton [1992], Cornell and Karlson [1997], Lawton [1999], and Srivastava [1999] for reviews). The present study is an experimental test of this conclusion with pond zooplankton.

METHODS

Experiment 1

This experiment was performed during the summer of 1997 in seven permanent fishless ponds at the W. K. Kellogg Biological Station of Michigan State University in Kalamazoo and Barry Counties, Michigan, USA. Six of the ponds were natural and one (Pond Lab; Table 2) was an artificial pond that had not been used in experiments or otherwise perturbed for >20 years (G. G. Mittelbach, *personal communication*). All of the ponds had maximum depths of 1–2 m. Ponds were separated by 0.3–10 km. The richness of the local crustacean and rotifer assemblages ranged from 16–22 species when the experiment was initiated, while regional richness among the seven ponds was 38 (11 crustaceans and 27 rotifers; Table 2, Appendix A). Whittaker's (1954) beta diversity (regional divided by local) ranged from 1.7–2.4 (mean = 2.0), indicating that 42–59% of the species present in any one of the seven ponds were initially found in each pond. The dominant predators of zooplankton in all ponds were insects (primarily *Chaoborus* spp., *Notonecta* spp., and *Neoplea striola*).

The experiment consisted of one treatment (the in-

vasion treatment) and a control replicated in each of the seven ponds. Enclosures were clear, cylindrical polyethylene bags, 1 m in diameter by 1 m deep (approximate volume of 800 L) suspended from the surface by Styrofoam floats, open to the atmosphere and closed to the sediments. There were three replicate bags per treatment in each pond. Bags were filled to capacity with pond water on 17–18 July by being submerged and then drawn up through the water column so that they received the resident planktonic community intact. Predators, floating macrophytes (primarily *Ceratophyllum* sp.), duckweeds, and detritus were enclosed at their ambient densities when the bags were filled. The bags were allowed to settle for 5–6 d before being subjected to experimental treatments.

The regional species inoculum was collected from 18 lakes and ponds including the seven in the experiment on 23 July. The volume filtered from each water body was adjusted to maximize evenness among species in the numbers of individuals introduced. The inoculum was gently mixed in a carboy and distributed into 50-mL aliquots, which were used to inoculate the bags. One aliquot was added to each bag in the invasion treatment. Three aliquots were fixed with Lugol's iodine solution to be counted. The remaining aliquots were heat-killed and one was added to each of the control bags in order to maintain equivalent nutrient balance between the invasion treatment and control. The aliquots were added to the bags within 4 h of collection to minimize stress to the organisms. Past experience and the work of other investigators (e.g., Vanni et al. 1997) have shown that zooplankton survive well with this minimal level of handling. Visual inspection of extra inocula indicated that the animals were alive and active; therefore, the introduced species were healthy at the time of introduction. Aliquots contained a mean of 12 species of crustaceans and 21 species of rotifers. On average, the ponds received 8.1 new species of crustaceans (i.e., species not found in the pond prior to inoculation) and 11.7 new rotifers (Appendix A).

Although effort was taken to include similar numbers of individuals of each species, many species (especially rotifers) were introduced in low numbers (<10 individuals per species, Appendix A). Many of these species were rare in every pond in the region. The average number of individuals per new species (i.e., ones not found in the initial samples) in the inocula was 34.4 for copepods (excluding nauplii and unidentifiable copepodid stages), 325.8 for cladocerans, and 5.5 for rotifers. Although cladocerans and rotifers are primarily asexual and therefore less susceptible than sexual taxa to Allee effects (positive density-dependent population growth) or stochastic extinction at low population sizes (Pimm et al. 1988), some species introduced in low numbers may have failed to invade because too few propagules were introduced. However, most species that were relatively abundant in any pond in the region

at the time of collection were well represented in the inoculum.

Zooplankton samples were taken during the day with 0.5 m long, 5 cm diameter PVC tube samplers that collected a column of water 0.4 m deep (mean volume of 0.82 L). Replicate subsamples were taken from 1–6 (mean = 3.1) haphazardly chosen locations in the bags and combined into a single sample in the field. The combined sample was filtered through an 80- μ m mesh and fixed in the field with Lugol's iodine solution. Although the same number of subsamples was collected from each bag in a pond on a given date, the volume sampled differed among ponds. This was necessary because ponds varied in the amount of macrophytes and detritus they contained. Large volumes could not be sampled from ponds with dense macrophytes and detritus without heavily contaminating the samples and greatly limiting the accuracy with which the samples could be counted. A different sampler was used for each bag in a pond to avoid contamination between bags, and samplers were thoroughly rinsed with well water and dried with a towel between ponds. Duplicate zooplankton samples were taken from the pond immediately outside the bags whenever the bags were sampled to test for enclosure effects. Bags were sampled on five dates over 90 d, including once on the day before the treatments were established (22 July). In Pond A, one enclosure in the invasion treatment was ruptured by an unknown animal; therefore only two replicates of the invasion treatment were analyzed. The experiment in Pond F was disturbed by ducks that began using the bags as resting structures after the second sampling date (day 33), resulting in considerable nutrient enrichment. Therefore, Pond F was not sampled after day 33. Because the enclosures did not show visible evidence of duck activity (i.e., guano or elevated chlorophyll concentrations) on day 33, data from the first two sampling dates were included in the analysis. Two zooplankton samples could not be counted as they were incompletely fixed and partly degraded by the time they were examined.

Water for chlorophyll *a* analysis was collected from each bag and duplicate samples were collected from the ponds (outside the enclosures) with plastic scoops on two dates (days 10 and 70). Water samples were filtered through Whatman GF/F filters (Whatman Incorporated, Clifton, New Jersey) and the filters extracted for 12 h in 95% ethanol at 4°C. The extracted samples were analyzed by fluorimetry (Welschmeyer 1994).

Zooplankton samples were counted under a dissecting microscope at 30 \times magnification. Higher magnification (75 \times) was used to identify species. Crustaceans, rotifers, and planktivorous insects (*Chaoborus* spp., notonectids, and pleids) were identified to the lowest possible taxonomic level according to Pennak (1978), Stemberger (1979), and Balcer et al. (1984). At least 200 individuals were counted from each sam-

ple whenever possible. Samples containing >500 individuals were subsampled with a wide bore pipette so that a subsample of known volume containing ~200 individuals was counted. The mean dry biomass of each species was estimated by measuring 20–55 individuals from haphazardly chosen samples and using the length–weight regressions for crustaceans and the length–volume relationships for rotifers in McCauley (1984). Fewer individuals of some rare species were measured. Population biomass was calculated for each species present in a sample by multiplying the abundance estimate by the species' mean body mass. Community biomass was calculated by summing population biomasses of all crustaceans and rotifers found in the sample.

Experiment 2

Experiment 2 was performed in four ponds during the summer of 1998 (Table 2). Two were semipermanent ponds, one at the Lux Arbor Reserve (Lux Arbor Pond 12) and the other at the Kellogg Biological Station Bird Sanctuary. The other two were permanent ponds in the Barry State Game Reserve, Barry County, Michigan. None of the ponds used in experiment 1 were used in experiment 2. A different enclosure design was used in experiment 2. The enclosures in experiment 2 were cylindrical cages, 0.8 m in diameter and 0.6 m deep, constructed from plastic-coated metal garden fencing. The cages were wrapped in the same type of polyethylene sheeting that was used to construct the bags in experiment 1. The cages were driven into the sediments so that they were exposed to the benthos but isolated from the rest of the pond. This design allowed the use of ponds shallower than 1 m deep. The enclosures were placed in ponds at a depth of 0.3 m and contained a volume of 150 L.

Nine enclosures were placed in each pond between 28 May and 30 May. A 153- μm mesh plankton net was passed 30 times through each enclosure in the resistance treatment on both 3 and 4 June. The enclosures in the control and invasion treatments were mixed with an oar for the same amount of time to control for the physical disturbance of filtering. Pretreatment zooplankton samples from all of the enclosures and duplicate samples from the ponds (outside the enclosures) were collected on 4 June. Two 750-mL subsamples were collected with plastic scoops from each enclosure and from the ponds outside the enclosures. The subsamples were combined into a single sample and fixed with Lugol's iodine solution in the field. A different scoop was used for each sample. An inoculum of invaders was collected from nine ponds around Kellogg Biological Station and added to the invasion and resistance treatments on the morning of 5 June. Heat-killed inocula were added to the control enclosures to control for nutrient addition. The ponds received an average of 24.3 new species (ones not present initially) in the inoculum with an average of 50.6 individuals

per species (Appendix B). The enclosures were sampled on 14 June and 14 July. Because 1998 was an exceptionally dry year, the pond levels dropped considerably and sampling was suspended after 14 July. Zooplankton samples were counted using the same methods as in experiment 1.

Data analysis

A species was considered invasive in a pond if it was absent prior to inoculation, was present in the inoculum, and only appeared in the invasion or resistance treatments (i.e., never in the control or the pond outside the bags) throughout the experiment. The control and pond samples served to distinguish between species that were experimentally introduced and those that appeared through the phenology of the ponds. Zooplankton show considerable species turnover throughout a season (Sommer 1989, Arnott et al. 1998); therefore I expected that new species would appear in the ponds that were not present initially. New species were found in the control and pond samples in all 11 ponds (Appendices A and B). These species were either present initially in numbers too low to be detected or else colonized the ponds from the sediments or from neighboring ponds. New species that appeared in the pond samples (outside the bags) generally appeared on the same date in the bags (*personal observation*); the bags therefore did not prevent species that may have emerged from the sediments from colonizing the bags. When species that appeared in the control and pond samples are excluded from the pool of potentially invasive species, the average number of new species introduced in the inoculum was 12.9 and 18.8 in experiments 1 and 2, respectively, and the average number of individuals per new species was 120.8 and 58.1 (Appendices A and B).

Invasibility was measured as the total biomass concentration and percent introduction success of exotic species. Percent introduction success was calculated for each sample as the number of exotic species present divided by the number of potentially exotic species in the inoculum. Potentially exotic species were defined as those that were absent from the pond prior to inoculation and never appeared in any control or pond samples in that pond throughout the experiment. All analyses were performed using SYSTAT version 8.0 (Wilkinson 1998). Patterns through time in the total biomass of exotic species in the invasion treatment in experiment 1 were tested by repeated-measures ANOVA for the four posttreatment sampling dates with pond as a factor. All effects were assumed to be fixed and Type III sums of squares were used. Pond was treated as a fixed effect in the repeated-measures ANOVA because ponds were chosen to represent a gradient in diversity and not a random sample of the ponds in the region (Newman et al. 1997). The biomass of exotic species was found to be nonnormal by a Lilliefors' test and so was $\log_{10}(x + 1)$ transformed. Only

the invasion treatment was analyzed by repeated-measures ANOVA since, by definition, the number of exotic species in the control and pond samples was always zero. Pond F was excluded from the repeated-measures ANOVA since the experiment ended in this pond after one month due to disturbance by ducks.

For experiment 1, effects of the invasion treatment and the enclosures on zooplankton species diversity (Fisher's alpha diversity index, including both resident and exotic species), total zooplankton biomass, native zooplankton biomass (all nonexotic species), and chlorophyll *a* concentration were tested by MANOVA with treatment and pond as factors (hypothesis 2, Table 1). Fisher's alpha index of diversity was used because it corrects for differences among samples in the number of individuals examined (Magurran 1988). The dependent variables for each replicate were calculated as the mean of all four posttreatment sampling dates. In Pond F, dependent variables were the means of the first two posttreatment sampling dates before the experiment was disturbed by ducks. The four dependent variables were all nonnormally distributed (Lilliefors' test, $P < 0.05$) and were therefore \log_{10} transformed. The levels for the treatment effect were control ($n = 3$), invasion treatment ($n = 3$), and pond ($n = 2$). When the MANOVA detected significant multivariate effects of pond or treatment, univariate ANOVAs were performed on the individual dependent variables with the level of significance adjusted by a Bonferroni correction (four dependent variables, $\alpha = 0.0125$).

To test correlations between local diversity and invasibility (hypothesis 3 in Table 1), each replicate value for a dependent variable was averaged over the post-treatment sampling dates. In Pond F, dependent variables were the means of the first two posttreatment sampling dates before the experiment was disturbed by ducks. The means of the time-averaged values for the three replicates were related to the diversity of the initial (pre-inoculation) zooplankton communities of the ponds by Spearman rank correlation. Initial diversity was calculated for each pond as the mean Fisher's alpha of all pond and enclosure samples, excluding the resistance treatment. Species richness (the cumulative number of species found among all the pretreatment samples) was also tested for correlations with invasibility to determine whether the choice of metric for diversity influenced the patterns observed. Since the a priori hypothesis was that invasibility would decline with resident diversity (Elton 1958, hypothesis 3 in Table 1), a one-tailed test of significance was used. All correlations were analyzed using data from experiment 1 alone and from both experiments together.

Effects of the invasion and resistance treatments (experiment 2) on the total biomass of exotic species (hypothesis 4 in Table 1) were analyzed by repeated-measures ANOVA for the two sampling dates (days 10 and 40) with treatment (invasion or resistance) and pond (H–K) as fixed factors. Effects of the treatments and

TABLE 3. Repeated-measures ANOVA for exotic species biomass in the invasion treatment (experiment 1).

Source	df	ss	F	P
Between subjects				
Pond	5	1.637	1.229	0.371
Error	9	2.397		
Within subjects				
Time	3	0.565	1.342	0.281
Time \times pond	15	2.964	1.408	0.213
Error	27	3.790		

Note: Pond F was excluded because the experiment was disturbed by ducks after the second sampling date.

enclosures on zooplankton diversity, total biomass, and native species biomass (hypothesis 2; Table 1) were analyzed by MANOVA where each replicate value for a dependent variable was averaged over the two sampling dates. Total and native zooplankton biomass were nonnormal (Lilliefors' test, $P < 0.05$) and so were \log_{10} transformed. Univariate ANOVAs were used to identify effects on individual variables when the MANOVA indicated a significant multivariate effect. The Bonferroni-adjusted significance level for the univariate ANOVAs was $\alpha = 0.017$.

RESULTS

Experiment 1

The effects of the invasion treatment among the seven ponds ranged from Pond A, where no introduced species was ever found, to Ponds B, F, and G, where one species consistently colonized all three replicate enclosures (Fig. 1). Averaged over the four sampling dates, the mean number of exotic species among the three bags in the invasion treatment ranged from 0 (Pond A) to 1.0 species (Pond G) with a mean of 0.4 species among the seven ponds. Percent introduction success ranged from 0 (Pond A) to 8.3% (Pond B; mean = 3.3%).

No significant differences among the four sampling dates were indicated by the repeated-measures ANOVA on the biomass of exotic species in the invasion treatment in experiment 1 (Table 3). Significant multivariate effects of treatment and pond were detected on the four dependent variables by MANOVA (Table 4A). However, none of the univariate ANOVAs indicated a significant effect of treatment (differences among the control, invasion, and pond samples) in any of the four dependent variables (all P values greater than the Bonferroni-adjusted α of 0.0125; Table 4 B–E).

The success of exotic species in the invasion treatments of the two experiments was negatively correlated with resident species diversity at the time of introduction (hypothesis 3; Table 1, Fig. 2). Both mean biomass of exotic species (Fig. 2A) and percent introduction success in the invasion treatment (Fig. 2B) declined with increasing resident species diversity. Exotic species biomass and percent introduction success were

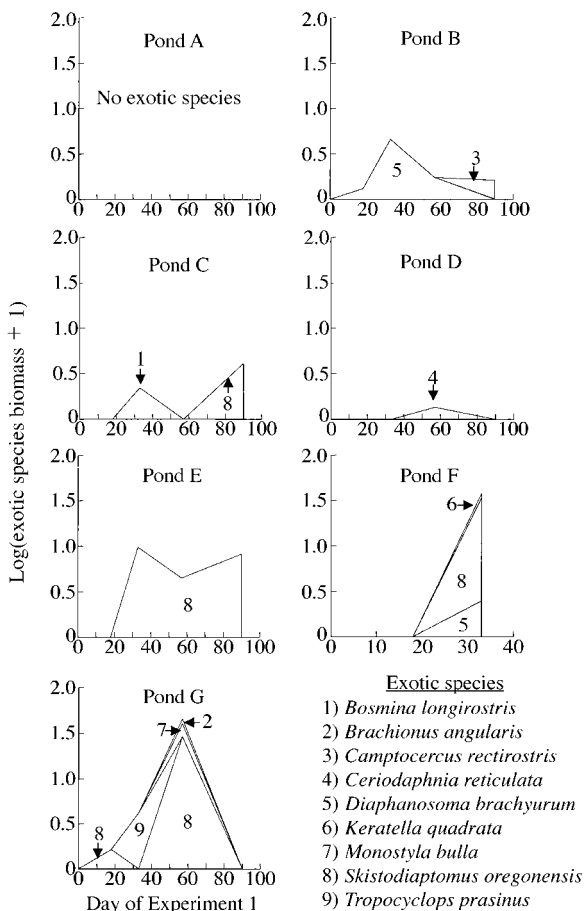


FIG. 1. Mean dry biomass of exotic species in the invasion treatment in experiment 1 through time. Each line represents the mean biomass of one exotic species among the three replicates. Numbers to identify species are given on the lower right. Values are means of $\log_{10}(\text{biomass} + 1)$; original units for biomass are micrograms per liter of pond water.

positively correlated ($r_s = 0.582$, one-tailed $P < 0.05$). Both measures of community invasibility were also negatively correlated with initial native species richness ($r_s = -0.630$, one-tailed $P < 0.025$ for exotic species biomass; $r_s = -0.520$, one-tailed $P < 0.10$ for percent introduction success).

Experiment 2

Repeated-measures ANOVA indicated that exotic species biomass was significantly greater in the resistance treatment than in the invasion treatment ($P = 0.002$; Table 5). No significant difference between the two sampling dates in total exotic species biomass in either treatment was detected by the repeated-measures ANOVA (Fig. 3, Table 5). MANOVA indicated significant multivariate effects of the treatments (control, invasion, resistance, and pond) and the ponds (H–K) on the three dependent variables (Table 6). The univariate ANOVAs found no significant effects of the

treatments or the enclosures on any of the dependent variables (Table 6).

Averaged over the two sampling dates, the mean number of exotic species among the three replicate enclosures of the invasion treatment in experiment 2 ranged from 0.3 (Pond H) to 0.8 species (Ponds J and K) with a mean of 0.6 species. Percent introduction success in the invasion treatment ranged from 1.8% (Pond H) to 4.4% (Pond J) with a mean of 3.3%. The mean number of exotic species found in the resistance treatment ranged from 1.8 (Pond J) to 2.8 species (Pond H) with a mean of 2.3 species while percent introduction success ranged from 9.5% (Pond K) to 15.6% (Pond I) with a mean of 12.4%. The total biomass of exotic species was, on average among the four ponds, 16.4 times greater in the resistance treatment than the invasion treatment (Fig. 3).

DISCUSSION

The hypothesis that dispersal limits the distributions of zooplankton among ponds (hypothesis 1, Table 1)

TABLE 4. (A) MANOVA test criteria for treatment and pond effects on characteristics of plankton communities in experiment 1. The table also presents results of univariate ANOVAs for (B) chlorophyll *a* concentration ($\mu\text{g/L}$), (C) total zooplankton diversity (Fisher's alpha), (D) total zooplankton biomass ($\mu\text{g/L}$), and (E) native zooplankton biomass ($\mu\text{g/L}$).

A) MANOVA test criteria (Wilks' lambda) and <i>F</i> statistics				
Source	Wilks' lambda	<i>F</i>	df	<i>P</i>
Pond	0.105	4.129	24, 109	<0.0001
Treatment	0.508	3.119	8, 62	0.005
Pond \times treatment	0.182	1.408	48, 121	0.069
Source	df	ss	<i>F</i>	<i>P</i>
B) Univariate ANOVA for chlorophyll <i>a</i> concentration ($\mu\text{g/L}$)				
Pond	6	6.365	8.284	<0.0001
Treatment	2	0.907	3.543	0.040
Pond \times treatment	12	1.926	1.253	0.290
Error	34	4.354		
C) Univariate ANOVA for total zooplankton diversity (Fisher's alpha)				
Pond	6	0.438	4.779	0.001
Treatment	2	0.030	0.973	0.388
Pond \times treatment	12	0.317	1.732	0.103
Error	34	0.519		
D) Univariate ANOVA for total zooplankton biomass ($\mu\text{g/L}$)				
Pond	6	4.878	7.775	<0.0001
Treatment	2	0.321	1.534	0.230
Pond \times treatment	12	2.629	2.096	0.045
Error	34	3.555		
E) Univariate ANOVA for native zooplankton biomass ($\mu\text{g/L}$)				
Pond	6	4.901	7.776	<0.0001
Treatment	2	0.311	1.482	0.241
Pond \times treatment	12	2.637	2.091	0.045
Error	34	3.572		

Notes: All dependent variables were averaged over all post-treatment sampling dates and \log_{10} transformed. Bold-faced *P* values are significant at the Bonferroni-adjusted level of significance of 0.0125.

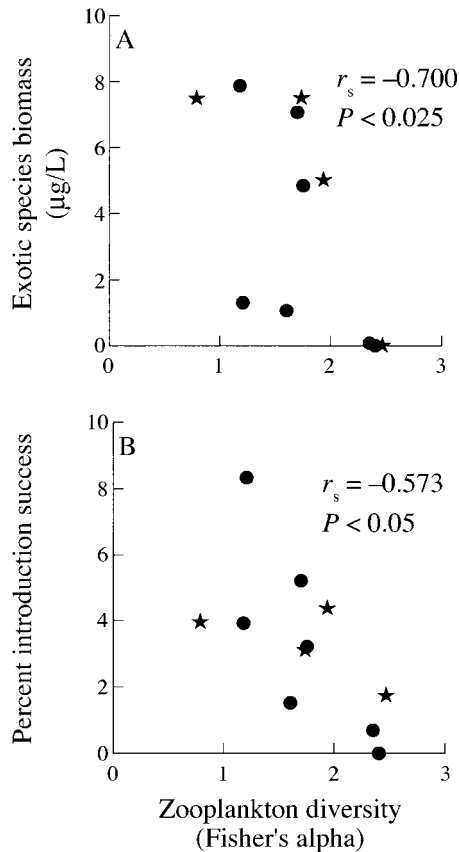


FIG. 2. The relationship between invasibility and diversity (hypothesis 3; Table 1): (A) total dry biomass of exotic species in the invasion treatment and (B) percent introduction success vs. initial species diversity (Fisher's alpha, crustaceans and rotifers). Circles are the ponds in experiment 1, and stars are the ponds in experiment 2. Fisher's alpha is the pretreatment mean of the pond and bag samples excluding the resistance treatment. Pond values for dependent variables are the mean values of the three replicates of the invasion treatment where each replicate value is averaged across all posttreatment sampling dates. P values are from a one-tailed test.

was supported by the result that species colonized the invasion treatment in ponds where they had been locally absent. Exotic species were found in the invasion treatment at least once in 10 of the 11 ponds in this study. The biomass of invasive species generally increased over the first month of experiment 1 in most ponds and remained fairly constant for the rest of the experiment (Fig. 1), although there was no significant effect of time in the repeated-measures ANOVA in either experiment (Tables 3 and 6). Because exotic species biomass did not decrease in the invasion treatment, these species were not sink populations in the process of becoming extinct. Since the durations of the experiments (90 and 40 d) were long relative to the generation times of most zooplankton (2–10 d, Lynch 1980, Stemberger and Gilbert 1985), the introduced species

most likely approached their approximate steady state abundance early in the experiments. Although it is not known whether populations of exotic species might have persisted over the long term, these species were at least able to maintain relatively constant numbers over several generations.

Although hypothesis 1 (Table 1) was supported by the result that introduced species colonized new ponds in the invasion treatments in both experiments, three lines of evidence suggest that dispersal limitation was not a major factor contributing to variation in zoo-

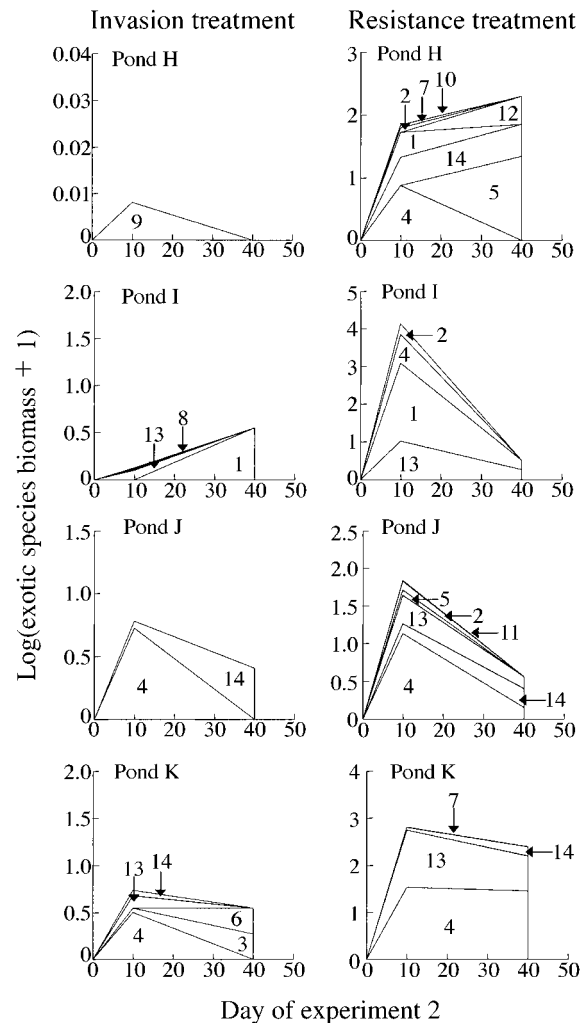


FIG. 3. Mean dry biomass of exotic species in the invasion (left panel) and resistance (right panel) treatments over time for the four ponds in experiment 2. Numbers refer to species as follows: (1) *Asplanchna* sp., (2) *Bosmina longirostris*, (3) *Chydorus sphaericus*, (4) *Daphnia dubia*, (5) *Diaphanosoma brachyurum*, (6) *Filinia longiseta*, (7) *Keratella cochlearis*, (8) *Lecane luna*, (9) *Monostyla closterocera*, (10) *Notholca laurentiae*, (11) *Pomphlox sulcata*, (12) *Sida crystallina*, (13) *Skistodiaptomus oregonensis*, and (14) *Tropocyclops prasinus*. Note that the scales of the y-axes differ among the graphs. Values are means of \log_{10} (biomass + 1); original units of biomass are micrograms per liter of pond water.

TABLE 5. Repeated-measures ANOVA for the effects of the invasion and resistance treatments on the dry biomass ($\mu\text{g/L}$) of exotic species in experiment 2.

Source	df	ss	F	P
Between subjects				
Pond	3	0.998	0.505	0.685
Treatment	1	9.681	14.710	0.002
Pond \times treatment	3	0.748	0.379	0.770
Error	14	9.213		
Within subjects				
Time	1	0.233	0.598	0.452
Time \times pond	3	0.724	0.620	0.613
Time \times treatment	1	0.424	1.088	0.315
Time \times trt \times pond	3	3.373	2.889	0.073
Error	14	5.449		

Notes: Biomass was $\log(x + 1)$ -transformed. Bold-faced *P* values are significant at the Bonferroni-adjusted level of significance of 0.017.

plankton community structure among these ponds. First, an average of only 0.5 exotic species was found among all bags in the invasion treatment in the two experiments. An average of 15.0 new species (ones that were absent initially and never occurred in control or pond samples) were introduced, therefore many of these species were likely excluded by local conditions. Although some species may have failed to establish due to stochastic extinction (Pimm et al. 1988), many species were introduced in sufficient numbers to be invulnerable to the problems of small populations (on average, 120.8 individuals per new species in experiment 1 and 58.1 in experiment 2, see Appendices). In addition, the high incidence and abundance of exotic species in the resistance treatment (Fig. 3) indicated that many species were excluded by interactions with resident species and not by stochastic extinction since the same numbers of individuals were introduced in both treatments. These results suggest that the majority of the species in the region capable of colonizing these ponds were already present.

The second result indicating that dispersal played a minor role in structuring the zooplankton communities of these ponds is that introduced species remained rare in every replicate in the invasion treatment. Exotic species made up only 0–2.5% (mean = 1.1%) of total zooplankton community biomass in experiment 1 and 0.03–0.65% (mean = 0.39%) in experiment 2. Since the ponds that were colonized did not support large populations, the exotic species were likely to have been vulnerable to subsequent extinction due to demographic or environmental stochasticity. Rare species are more susceptible to extinction (Pimm et al. 1988) and therefore dependent on dispersal from the region to maintain local populations (the rescue effect, Gilpin and Hanski 1991).

The third line of evidence suggesting that dispersal limitation played a smaller role than local processes in structuring zooplankton communities in these ponds is that exotic species had no detectable effects on char-

acteristics of the communities they invaded (hypothesis 2). Relaxing dispersal limitation had no apparent impact on total zooplankton biomass or diversity, or on the biomass of resident species in any of 11 ponds in two experiments. In addition, there were no effects of the invasion treatment on chlorophyll *a* concentration in experiment 1. These results suggest that dispersal does not strongly limit species diversity or community biomass in zooplankton or have a major influence on phytoplankton biomass. They also provide no indication that native species were affected by the invasion of new species from the region. The lack of measurable effects of the introduced species on characteristics of the invaded communities is not surprising given their relatively low biomass in every replicate of the invasion treatment. These results support observational evidence that most exotic species have minimal impacts on invaded communities (Williamson and Fitter 1996).

One implication of the result that pond zooplankton communities resisted invasion by many species in the regional pool is that colonization rates greatly exceed the probability of local extinction for most species. Several lines of evidence suggest that this is the case for zooplankton. First, the cosmopolitan distributions of many species have long been assumed to indicate

TABLE 6. (A) MANOVA test criteria for treatment and pond effects on characteristics of plankton communities in experiment 2. The table also presents results of univariate ANOVAs for (B) total zooplankton biomass ($\mu\text{g/L}$), (C) native zooplankton biomass ($\mu\text{g/L}$), and (D) total zooplankton diversity (Fisher's alpha).

A) MANOVA test criteria (Wilks' lambda) and <i>F</i> statistics				
Source	Wilks' lambda	<i>F</i>	df	<i>P</i>
Pond	0.059	15.545	9, 63	< 0.0001
Treatment	0.346	3.856	9, 63	0.0006
Pond \times treatment	0.253	1.702	27, 76	0.037
Source	df	ss	<i>F</i>	<i>P</i>
B) Univariate ANOVA on log total zooplankton dry biomass ($\mu\text{g/L}$)				
Pond	3	7.733	53.200	< 0.0001
Treatment	3	0.229	1.578	0.217
Pond \times treatment	9	1.288	2.953	0.013
Error	28	1.357		
C) Univariate ANOVA on log native zooplankton dry biomass ($\mu\text{g/L}$)				
Pond	3	7.997	49.472	< 0.0001
Treatment	3	0.256	1.585	0.215
Pond \times treatment	9	1.286	2.652	0.023
Error	28	1.509		
D) Univariate ANOVA on total zooplankton diversity (Fisher's alpha)				
Pond	3	10.613	21.289	< 0.0001
Treatment	3	1.855	3.720	0.023
Pond \times treatment	9	0.330	0.220	0.989
Error	28	4.653		

Notes: Total and native zooplankton biomass were \log_{10} transformed. Bold-faced *P* values are significant at the Bonferroni-adjusted level of significance of 0.017.

that zooplankton disperse effectively over large distances (Pennak 1978). Dormant life history stages have often been assumed to be the primary mode of dispersal and to account for the large geographic ranges of many zooplankton (Pennak 1978). In addition, diapausing eggs allow species to disperse through time as well as through space, providing a second mechanism by which populations can be reestablished following local extinction (De Stasio 1990). The rapid spread of some exotic zooplankton also suggests that these species disperse effectively across large distances (Havel et al. 1995). Finally, two experimental studies of zooplankton succession found that many species quickly invaded new habitats. Jenkins and Buikema (1998) constructed 12 experimental ponds and allowed them to be colonized naturally by species from the region. Fifty-seven crustacean and rotifer species invaded the ponds over one year. Local richness increased for the first 6–7 months after the ponds were constructed and remained constant thereafter (Jenkins and Buikema 1998, Fig. 3). This pattern indicates that local zooplankton communities quickly achieved a balance between colonization and extinction. Similarly, in an experiment at Kellogg Biological Station where artificial pools were placed at four distances (5, 10, 30, and 60 m) from two natural ponds, we found that, on average, 0.25 new species colonized the pools per day (J. B. Shurin and G. M. Cohen, *unpublished data*). In addition, distance from the source pond had a very weak effect on the rate at which new species arrived, suggesting that most species disperse broadly over distances up to 60 m. Taken together, these studies provide strong evidence that zooplankton move rapidly among ponds separated by relatively short distances.

Although dispersal played a relatively weak role in constraining species distributions among ponds within an area of $\sim 100 \text{ km}^2$, the importance of dispersal limitation is expected to increase at greater regional extents. Drawing species for the regional pool from more ponds over larger areas increases the number of potential invaders according to the familiar species-area relationship (Shurin et al. 2000). A larger pool of introduced species might increase the number of successful invasions and possibly the impact of exotic species on the local communities as well. That is, species are more likely to be excluded by limited dispersal from ponds separated from source populations by long distances than by shorter distances. The results of the present study suggest that dispersal played a relatively minor role in generating observed differences in community structure among these 11 ponds. It is important to remember that this conclusion applies only to the scale (100 km^2) at which the regional pool was defined.

Evidence for weak dispersal limitation in zooplankton contrasts with studies of terrestrial plant (Burke and Grime 1996, Tilman 1997) and intertidal invertebrate communities (Roughgarden et al. 1988). Investigations in these systems have found the supply of

species from the region greatly limits local diversity and has large effects on community structure. One potential explanation for this disparity is that sessile species require one propagule to colonize each microsite. A single asexual zooplankton can potentially colonize an entire pond, therefore fewer propagules may be necessary to saturate the environment. In addition, recruitment of sessile species may be limited by environmental heterogeneity at very small scales. That is, suitable microsites for barnacle settlement or seedling germination are likely on the order of centimeters. In this case, successful establishment of a colonist depends on where it lands in a fine-scale mosaic. In contrast, motile organisms such as zooplankton can explore the full range of heterogeneity in a pond and may therefore experience greater establishment success upon arrival.

The invasion treatment was performed in multiple ponds in order to test Elton's (1958) hypothesis that diversity confers resistance to invasion by correlating invasibility with native species diversity among ponds. Empirical tests of this hypothesis have yielded mixed results. Some observational studies have found that the number of invasive species on islands decreases with increasing native species richness (see Case and Bolger 1991 for an example with reptiles) while others have found no relationship between native diversity and the incidence of exotic species (Case 1996, Duncan 1997). Recently, Stohlgren et al. (1999) showed that the relationship between the number of exotic weeds and native species richness varied among several types of plant communities. Similarly, experimental tests of Elton's (1958) hypothesis have found negative (McGrady-Steed et al. 1997, Tilman 1997), positive (Robinson et al. 1995), and no effects (Robinson and Dickerson 1984) of diversity on invasibility. Recent modeling has shown that the relationship between diversity and invasibility depends on the processes that maintain diversity in the target community (J. Moore, *personal communication*). The mixed support for Elton's hypothesis may reflect differences in the underlying mechanisms for species coexistence in different types of organisms. The relationship between diversity and invasibility may provide clues as to the processes that influence diversity in different communities.

Two mechanisms can make species-rich communities less prone to invasion. The first is the sampling artifact that the likelihood an immigrant belongs to a new species decreases as local diversity increases. The second is that the number of potential interspecific interactions, either through direct trophic links or shared resources or predators, increases with species richness. More species interactions may lead to a greater community-wide strength of interaction and possibly to greater invasion resistance as well (Elton 1958, Pimm 1989, Case 1990, Robinson et al. 1995, Tilman 1997). If the second mechanism is important in determining community invasibility, then the biomass of exotic spe-

cies once established is expected to be lower in more diverse communities because fewer free resources will be available. In addition, the per species introduction probability of invasion success is expected to decline with increasing resident diversity. Dividing the number of successful invasions by the number of species introduced corrects for the sampling artifact described above. This experiment supported both predictions. The biomass of exotic species and percent introduction success in the invasion treatment both declined with increasing resident species diversity (Fig. 2). These patterns are consistent with the hypothesis that less diverse communities are more easily invaded by new species (hypothesis 3). Although invasibility and resident species diversity were negatively correlated, natural variation in diversity is confounded with variation in species composition (Huston 1997). It is therefore possible that correlations between invasibility and diversity are driven by the identities or traits of the species present and not by diversity per se. More mechanistic experiments in which the diversity and composition of the target communities are manipulated independently are needed to determine their roles in affecting invasibility.

The patterns of declining invasibility with increasing resident diversity suggest that interactions with native species excluded many introduced species from the invasion treatment. The contrast between the invasion and resistance treatments confirmed that many potential invaders were repelled by interactions with the local biota (hypothesis 4; Fig. 3). Averaged among the four ponds in experiment 2, the number of exotic species was 3.8 times greater while their total biomass was 16.4 times greater in the resistance treatment than in the invasion treatment (Fig. 3, Table 5). This result indicates an important role for species interactions in repelling invaders and strengthens the conclusion that local processes exert strong influence (relative to dispersal) in structuring zooplankton communities. In addition, the plankton net used to remove zooplankton had a large mesh size (153 μm). Filtering had a visually obvious effect on large species, however many small species such as rotifers remained abundant in the resistance treatment (*personal observation*). The magnitude of the effect of the resistance treatment is therefore a conservative estimate of the role of species interactions in deterring invaders. More sophisticated manipulations of target communities (e.g., of specific community members) are necessary to determine the nature of the biotic and abiotic factors that exclude invaders from ponds.

The conclusions of the present study contrast with one interpretation of patterns of local and regional species richness. A companion study (Shurin et al. 2000) showed that local crustacean species richness is a positive, linear function of the number of species in the surrounding region. Similar patterns have been documented for a diverse array of organisms (reviewed in

Cornell and Karlson 1997, Lawton 1999, Srivastava 1999). One potential explanation for linear patterns of local and regional richness is that communities are open to invasion by species from the region. Such relationships have often been interpreted to indicate that local processes in general and interspecific interactions in particular are of minor importance in constraining species distributions among sites (Ricklefs 1987, Cornell and Lawton 1992, Cornell and Karlson 1997, Lawton 1999). However, other explanations may account for patterns of local and regional diversity (e.g., Cornell and Lawton 1992, Caswell and Cohen 1993, Huston 1999). Shurin et al. (2000) discuss alternative hypotheses in greater detail. The present study showed that zooplankton communities resisted invasion by most new species within a region of 100 km². In addition, the resistance treatment showed that biotic interactions played a major role in excluding potential colonists from ponds (hypothesis 4; Fig. 3). These results suggest that linear, positive relationships between local and regional species richness do not indicate that dispersal plays a dominant role, relative to local processes, in structuring communities. Other types of evidence will be necessary to draw inferences about the roles of local and regional processes.

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APPENDIX A

A list of the taxa identified in experiment 1 is available in ESA's Electronic Data Archive: *Ecological Archives* E081–026-A1.

APPENDIX B

A list of the taxa identified in experiment 2 is available in ESA's Electronic Data Archive: *Ecological Archives* E081–026-A2.