

Dispersal Rates Affect Species Composition in Metacommunities of *Sarracenia* *purpurea* Inquilines

Jamie M. Kneitel* and Thomas E. Miller†

Department of Biological Science, Florida State University,
Tallahassee, Florida 32306-1100

Submitted June 6, 2002; Accepted February 20, 2003;
Electronically published July 21, 2003

ABSTRACT: Dispersal among local communities can have a variety of effects on species composition and diversity at local and regional scales. Local conditions (e.g., resource and predator densities) can have independent effects, as well as interact with dispersal, to alter these patterns. Based on metacommunity models, we predicted that local diversity would show a unimodal relationship with dispersal frequency. We manipulated dispersal frequencies, resource levels, and the presence of predators (mosquito larvae) among communities found in the water-filled leaves of the pitcher plant *Sarracenia purpurea*. Diversity and abundance of species of the middle trophic level, protozoa and rotifers, were measured. Increased dispersal frequencies significantly increased regional species richness and protozoan abundance while decreasing the variance among local communities. Dispersal frequency interacted with predation at the local community scale to produce patterns of diversity consistent with the model. When predators were absent, we found a unimodal relationship between dispersal frequency and diversity, and when predators were present, there was a flat relationship. Intermediate dispersal frequencies maintained some species in the inquiline communities by offsetting extinction rates. Local community composition and the degree of connectivity between communities are both important for understanding species diversity patterns at local and regional scales.

Keywords: dispersal frequency, metacommunity, *Sarracenia purpurea*, protozoa, local and regional diversity.

The role of dispersal in determining species diversity in communities composed of patchy habitat (metacommunities)

has long been recognized (Huffaker 1958; Simberloff and Wilson 1970; Horn and MacArthur 1972; Caswell 1978; Case 1991; Hanski 1999). In the absence of dispersal among local communities, low local diversity is expected because dominant competitors or predators in each patch drive other species to extinction (fig. 1). As dispersal among patches increases to some intermediate level, an increase in local diversity is expected for two reasons (Caswell 1978; Caswell and Cohen 1991; Loreau and Mouquet 1999; Mouquet and Loreau 2002). First, as dispersal frequency increases, dispersal-limited species enter new patches. Second, increasing dispersal rates can maintain some rare species (which are typically driven to extinction quickly) in local communities as transient fugitives or by a rescue effect (Brown and Kodric-Brown 1977; Shmida and Wilson 1985; Pulliam 1988; Loreau and Mouquet 1999; Mouquet and Loreau 2002). An assumption underlying this prediction is that the rate to competitive exclusion is slower than the dispersal events. However, very high dispersal frequencies effectively create one large community (Levin 1974; Taylor 1988; Mouquet and Loreau 2002) and allow a regionally dominant competitor to constantly invade each local community, thereby reducing local diversity in all patches (Caswell 1978; Taylor 1988; Amarasekare and Nisbet 2001; Forbes and Chase 2002; Mouquet and Loreau 2002). Overall, this logic predicts a hump-shaped relationship between dispersal frequency and local species richness (fig. 1).

The prediction presented in figure 1 assumes strong interactions between species, but the strength of these interactions may depend on local community conditions. For example, a decrease in competition might be related to resource levels (Tilman 1982; Waide et al. 1999) or to a predator that suppresses the dominant competitor (Paine 1966; Leibold 1996; Shurin and Allen 2001). This decrease in competition might then lead to increases in diversity and thereby raise the curve (fig. 1). Another hypothesis is that the hump shape might be lowered by an increase in competition with reduced resource levels or when species

* Present address: Washington University, Tyson Research Center, P.O. Box 258, Eureka, Missouri 63025; e-mail: kneitel@biology2.wustl.edu.

† E-mail: miller@bio.fsu.edu.

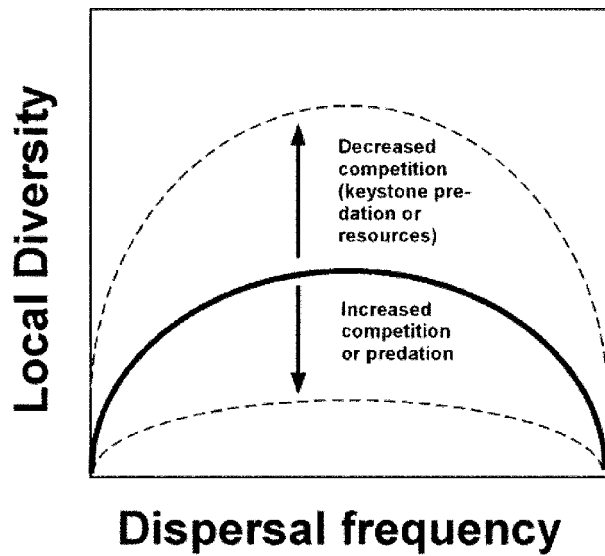


Figure 1: Predicted relationship between dispersal frequency and species diversity (modified from Mouquet and Loreau 2002). This relationship may be altered by local conditions. Increases in resources or keystone predation may elevate this relationship by reducing competition. Alternatively, increased competition or direct exclusion by predators may dampen this relationship.

are excluded by predators (fig. 1). Interestingly, predators can enhance diversity at the regional scale while either enhancing or reducing diversity at the local community scale depending on the colonization and extinction rates of competing species and their predators (Shurin and Allen 2001).

The inquiline communities that inhabit the modified leaves of the purple pitcher plant, *Sarracenia purpurea*, provide an excellent system in which to test the importance of dispersal in structuring communities within a meta-community context. Leaves are produced approximately every 2 mo and may maintain active communities for 1–2 yr (T. E. Miller, unpublished data). These leaves form the habitat for a small community of aquatic organisms (Addicott 1974; Harvey and Miller 1996). The resource base is made up of invertebrates that drown in the water-filled pitchers. Detritivores, like mites and chironomids, consume carcasses directly, but bacteria are the primary decomposers that feed higher trophic levels. The middle trophic level is composed of numerous species of protozoa and very few species of rotifers, most notably the pitcher plant obligate *Habrotrocha rosa*. In contrast to previous presentations of this food web, rotifers do not appear to eat protozoa in this system, based on behavioral and gut observation (Bledzki and Ellison 1998; J. M. Kneitel, unpublished data). The top predator in this system is most commonly the larvae of the pitcher plant mosquito, *Wyeo-*

myia smithii (Addicott 1974; Cochran-Stafira and von Ende 1998; Kneitel and Miller 2002), which can subsist on bacteria but primarily consumes protozoa and rotifers (Kneitel 2002).

These species naturally colonize leaves on a time scale of days to weeks (J. M. Kneitel, unpublished data). The method of dispersal varies among inquiline species: dipteran larvae are oviposited (Istock et al. 1975; Heard 1994), while others arrive passively by dormant propagules or splashing from adjacent pitchers (Maguire 1963; Revill et al. 1967; Caceres and Soluk 2002). Extinction rates in this system can be highly variable and can range from a couple of days to months (Luckinbill 1979; Drake 1991; Lawler and Morin 1993; Burkey 1997; J. M. Kneitel, unpublished data). Therefore, dispersal frequencies (as colonization events per leaf) on the order of weeks can have significant effects on species interactions and community dynamics. Previous work has shown that competition and predation are important in this system (Addicott 1974; Cochran-Stafira and von Ende 1998; Kneitel and Miller 2002) and that protozoan species' invasions can be limited or facilitated by the presence of competitors and predators (Miller et al. 2002). Protozoan species diversity has been found to be negatively affected by predation (Addicott 1974; Kneitel and Miller 2002) and positively affected by resource additions (Kneitel and Miller 2002). Therefore, resources may further enhance the effects of dispersal by increasing species diversity (fig. 1).

The purpose of our study was to test the predictions of the conceptual model presented in figure 1. We conducted a field experiment examining the effects of dispersal frequency on species diversity and abundances at local and regional scales of the *S. purpurea* inquiline community. Resource and predator density levels were also manipulated to determine whether dispersal frequencies interact with local community conditions in affecting protozoan species richness.

Methods

Sarracenia purpurea, the purple pitcher plant, occurs in bogs and wetlands from Florida to Canada. The present study was conducted in a population of *S. purpurea* at the Mud Swamp site in the Apalachicola National Forest, 6 km northeast of Sumatra, Florida (30°N, 84°W).

Experimental Design

The $3 \times 2 \times 3$ factorial design included three levels of resource input (none, five ants, and 25 ants), two levels of predator addition (five *Wyeomyia smithii* larvae present and predators absent), and three frequencies of dispersal among pitchers (none, every 2 wk, and weekly). The re-

source and predator treatment levels were chosen to reflect the range of ambient densities (Kneitel and Miller 2002). Autoclaved fire ants (*Solenopsis invicta*) were used as prey because they are the insect prey most commonly found in local pitchers (Miller et al. 1994; Kneitel and Miller 2002). For the migration treatment, each of the treatment replicates consisted of a set of five pitchers among which migration was implemented at the appropriate frequency. One replicate of each of the 18 treatment combinations was randomly applied within each of five haphazardly located blocks.

We prepared treatments in the laboratory by placing 15-mL aliquots of sterile water in separate vials. Appropriate densities of resources and predators were added to each randomly assigned vial. In the field, 90 healthy leaves on individual plants were marked in each of five blocks. The treatment leaves were of approximately equal size and were washed out repeatedly with sterile water just before use. The contents of the treatment vials prepared in the lab were then poured into the appropriate leaves in the field.

Mesh cloth (1 mm) was placed over the mouths of the treated pitchers to prevent further prey entry or ovipositing by mosquitoes. We allowed 10 d before initiating dispersal treatments to allow communities to become established. Sterilized ants and mosquito larvae were replenished in the appropriate resource and predator treatments after 4 wk.

In the weekly and biweekly dispersal treatments, one 0.5-mL sample was taken from each of the five pitchers in a treatment set, and then the five samples were pooled. This "pool" was gently mixed, and 0.25 mL was put back into each pitcher of that set (approximate number of protozoan individuals colonizing: mean = 2,889, SE = 498). The remainder of the pool was taken to the laboratory for analysis.

Sampling

The experiment began June 11, 2001, and subsampling occurred each week for 8 wk. At week 8, all experimental pitchers were sampled. Protozoan abundance and species richness and rotifer abundance were determined from 0.1-mL sample in a Palmer cell counter under a compound microscope ($\times 100$). Protozoans were identified to genus (Pennak 1989; Patterson 1996), and rotifers consisted almost entirely of *Habrotrocha rosa*.

Statistical Analyses

The richness and abundance means of each replicate set from week 8 were used to quantify treatment effects. The among-set variance of each replicate set was used to determine the degree of similarity in each treatment. Indi-

vidual species data were normalized by log transformation. Regional protozoan richness data were normalized with a square root transformation. Four-way mixed-model ANOVAs were conducted in which resources, predators, and dispersal frequency were fixed independent variables; block was a random independent variable. The dependent variables consisted of local and regional protozoan species richness, local protozoan species richness variance, total local abundance of protozoa, and local abundance of common rotifers and protozoa. Only one case (local species richness) revealed an interaction between treatments. In all others, interaction terms were dropped from analyses (Zar 1996), which ultimately had no effect on the results. To test for differences among individual treatments, we conducted Bonferroni-adjusted post hoc tests.

Treatments produced substantial variation in species abundances, and treatments with more individuals may have artificially inflated species richness (Gotelli and Graves 1996). Therefore, to compare treatments directly while controlling for abundance differences, we conducted rarefaction to estimate local species richness of protozoa (EcoSim, ver. 6; Gotelli and Entsminger 2001). We randomly sampled 800 individuals from each sample. Some replicates had fewer individuals, and the total sample was used, generally none to two species. Each replicate was sampled 100 times, and the average number of species was used as our estimate. Rarefaction curves were generated for each replicate, and the final point in each curve was used as the dependent variable in our analyses.

Results

After 8 wk, 51 of the 450 pitchers had been damaged (pierced or torn) and were eliminated from the study. These communities were not replaced, so some sets of pitchers linked by migration consisted of four or, in one case, three pitchers by the end of the experiment.

In all, 34 protozoan taxa were collected during this experiment. Regional species richness of protozoa increased with increasing dispersal rates and was increased marginally significantly ($P < .06$) with increasing resources (table 1; fig. 2A). Block also significantly affected regional and local species richness.

Local protozoan diversity was significantly affected by the main effects of predator addition and dispersal frequency (table 1; fig. 2B). A significant interaction between dispersal and predation was detected ($F = 3.96$, $P = .02$; fig. 2B). When predators were absent, richness was highest at intermediate levels of dispersal, but richness did not change with dispersal frequency in the presence of predators (fig. 2B). Local richness was significantly greater in the absence than in the presence of predators only at low levels of dispersal. Interestingly, variance among pitch-

Table 1: Results from four-way ANOVAs for protozoan richness, variance, total abundance, and protozoan and rotifer abundance

Dependent variable	Resource df = 2	Predator df = 1	Dispersal df = 2	Block df = 4
Regional richness	2.97*(I)	2.79	3.06*(I)	3.58**
Local richness	2.29	4.09*(D)	3.76*(I)	3.16*
Local variance	.41	2.76	3.34*(D)	.32
Total abundance	2.79	3.11	8.89***(I)	2.79*
<i>Bodo</i>	1.90	5.39*(I)	3.19*(I)	2.73*
Chryomonad	1.68	.32	2.95*(I)	2.34*(*)
<i>Colpidium</i>	5.66**(I)	.40	3.54*(I)	3.69**
<i>Colpoda</i>	1.34	.51	3.63*(I)	2.15
<i>Cyclidium</i>	.41	1.30	2.29	2.21
<i>Paramecium</i> A	11.14***(I)	.01	2.76	1.23
Rotifers	18.03***(I)	5.41*(D)	1.12	4.58**

Note: *F* values are given for each dependent variable. Parentheses around asterisks indicate marginally nonsignificant *P* values ($P < .06$). Direction of effect: (I) = increase; (D) = decrease.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

ers significantly decreased with increasing dispersal frequency (table 1; fig. 2C).

Total protozoan abundance increased significantly with increasing dispersal levels (table 1; fig. 2D), by 37% at low dispersal levels and 46% at high dispersal levels. This was reflected in some of the common protozoans species: *Bodo*, Chryomonad, *Colpidium*, and *Colpoda* (table 1). The most common protozoan species also showed different responses to the other treatments. Abundance of *Colpidium*, *Paramecium* A, and rotifers increased with increasing resource levels (table 1). In the presence of predators, abundance of *Bodo* increased and that of rotifers decreased significantly, a pattern seen previously (Kneitel and Miller 2002).

Discussion

In the pitcher plant inquiline system, dispersal among local communities did significantly affect both local and regional richness (table 1). At the regional scale, increases in dispersal led to an increase in richness and decrease in variance among local communities within a region. Further, there was a significant interaction between dispersal rate and the presence of predators: when predators were removed, there was a hump-shaped relationship between dispersal frequency and local richness, consistent with part of the model in figure 1. In the presence of predators, there was a flat relationship between local diversity and dispersal frequency.

We can draw some further support for the model by considering the mechanisms involved in figure 1. In the absence of dispersal, local richness is predicted to be re-

stricted by increased extinction rates due to predation, competition, or both. In this study, local abundance of most of the species was lowest when there was no dispersal among local communities (table 1; fig. 2D); the probability of local extinction is likely to be highest when local abundances are low. These patterns reflect those seen in closed and linked communities in other systems (Huffaker 1958; Shorrocks 1991; Holyoak and Lawler 1996; Burkey 1997; Gonzalez et al. 1998; Shurin 2001).

As dispersal among local communities increases, the model predicts that local and possibly regional richness will increase as dispersal limitation is overcome, population abundances increase, and rates of local extinction decrease. This prediction was borne out by the data (table 1), as both local and regional richness increased with dispersal. Increased dispersal apparently reduced extinctions, increasing the average local abundances of many component species (table 1; fig. 2D). However, increased dispersal rates had no effect on local diversity when *Wyeomyia smithii* was present, which may have resulted from the direct effect of predation on extinction rates or the success of invasion (Shurin 2001; Miller et al. 2002).

The model predicts that very high rates of dispersal should lead to reduced local diversity as some species begin to dominate across all local communities, decreasing both α and β diversity. This pattern is found when predators are excluded: local diversity declines at the highest dispersal levels (fig. 2B) and variance in local richness decreases (table 1; fig. 2C). In fact, variance appeared to decrease the most between no dispersal and low dispersal levels, despite an increase in local and regional richness. Similarly, Gilbert et al. (1998) found that when dispersal was present, there was an increase in the homogeneity among local patches while regional diversity increased. Increases in species richness among patches that accompany homogenization of species composition may result when there are weak interactions among species, nontransitive competition, or rescue effects.

Previous work in this system has shown that resource addition leads to increased local diversity (Kneitel and Miller 2002) and to increased rates of invasion (Miller et al. 2002), perhaps due to a reduction in competitive intensity. However, in this study, we found no effect of added resources on local diversity and no evidence of an interaction between dispersal and resources as predicted (fig. 1; see also Mouquet and Loreau 2002), despite the response of individual species (table 1). The conflict between this study and previous work may be due to significant among-field or among-year variation in the effects of resource addition.

In metacommunities, species colonization and extinction rates among ephemeral patches contribute to local and regional community dynamics. Dispersal among local

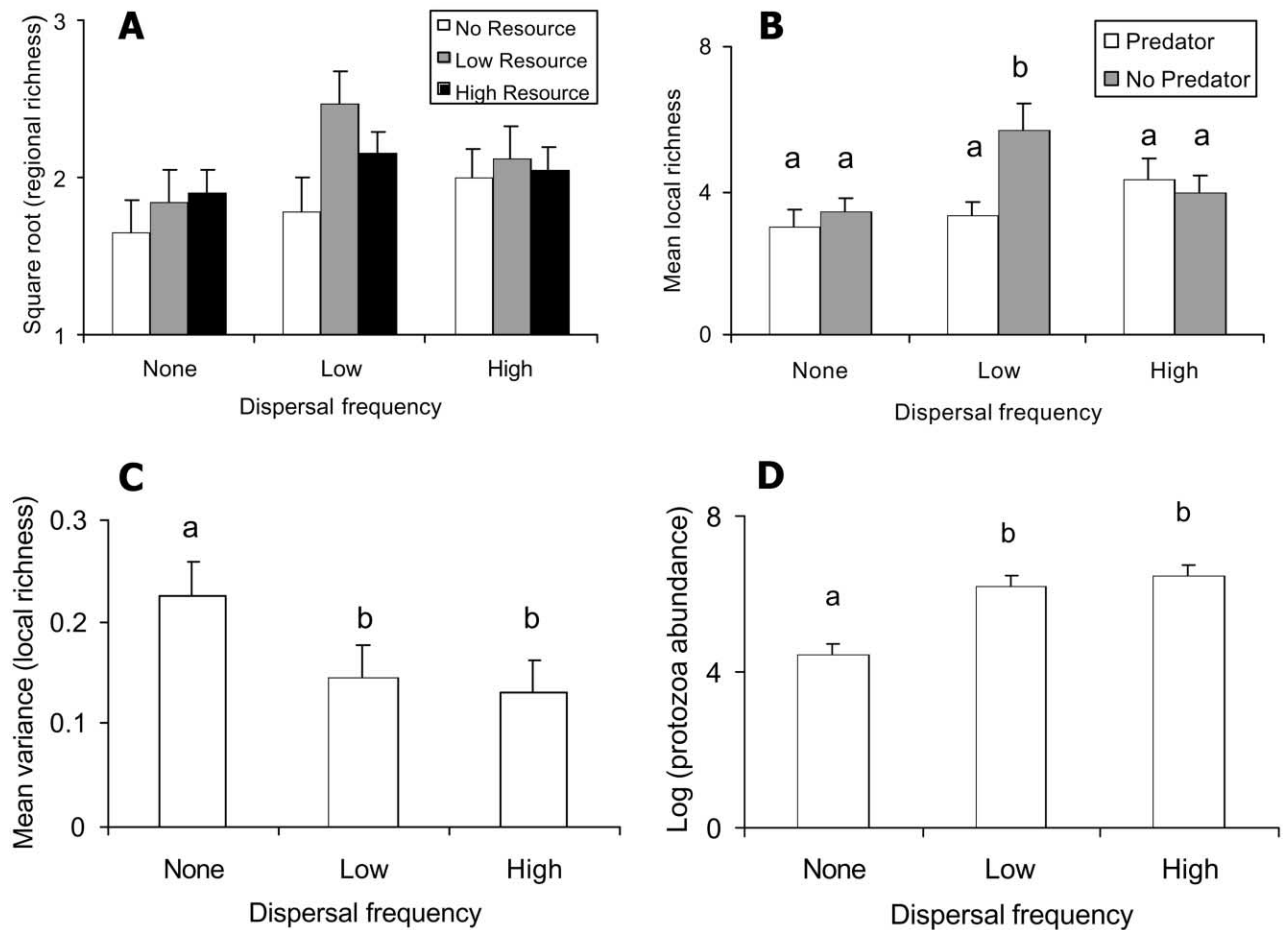


Figure 2: A, Mean (± 1 SE) protozoan regional species richness (square root transformed) in resource and dispersal-frequency treatments. B, Local species richness (rarefied) in predator and dispersal-frequency treatments (the interaction term between these treatments was significant). C, Variance of local richness (among the set of five pitchers in each replicate treatment) in the dispersal-frequency treatments. D, Total protozoan abundance (log transformed) in the dispersal-frequency treatments. In B–D, bars with the same lowercase letter are not significantly different between treatments at $P = .05$.

communities is known to influence community structure in numerous theoretical (MacArthur and Wilson 1967; Caswell 1978; Loreau and Mouquet 1999), laboratory microcosm (Holyoak and Lawler 1996; Warren 1996a, 1996b), and recent field studies (Gonzalez et al. 1998; Shurin 2000; Forbes and Chase 2002). Most empirical studies examine the effects of introducing novel species into otherwise closed communities or follow natural colonization events in local communities. Our study directly manipulated the frequency of dispersal among a group of local communities, allowing us to quantify both local and regional effects. Our results are consistent with the conceptual model presented: a unimodal diversity-dispersal relationship was found when predators were absent. Competitive exclusion was likely overcome by increasing dispersal through rescue or mass effects. Mosquitoes

seemed to directly exclude species rather than act as a keystone predator, as indicated by the flat dispersal-diversity relationship in their presence. The present study highlights our need to consider the relative rates of dispersal and extinctions in order to understand community dynamics. While we could not directly measure extinction rates, the study does provide strong evidence for the role of dispersal frequencies and species interactions in determining diversity patterns at both local and regional scales.

Acknowledgments

D. Arellano, E. Boyd, H. Buckley, B. Lawton, M. Wise, and S. Yinger made this project possible with their blood, sweat, and tears, but mostly with sweat. Comments by J. Shurin and an anonymous reviewer smoothed out the

rough edges and improved the article. This project was funded by National Science Foundation grants DEB-0083617 and DEB-0091776 to T.E.M.

Literature Cited

- Addicott, J. F. 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., and R. M. Nisbet. 2001. Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. *American Naturalist* 158:572–581.
- Bledzki, L. A., and A. M. Ellison. 1998. Population growth and production of *Habrotrocha rosa* Donner (Rotifera: Bdelloidea) and its contribution to the nutrient supply of its host, the northern pitcher plant *Sarracenia purpurea* L. (Sarraceniaceae). *Hydrobiologia* 385:193–200.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445–449.
- Burkey, T. V. 1997. Metapopulation extinction in fragmented landscapes using bacteria and protozoa communities as model ecosystems. *American Naturalist* 150: 568–591.
- Caceres, C. E., and D. A. Soluk. 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. *Oecologia* (Berlin) 131:402–408.
- Case, T. J. 1991. Invasion resistance, species buildup and community collapse in metapopulation models with interspecies competition. *Biological Journal of the Linnean Society* 42:239–266.
- Caswell, H. 1978. Predator-mediated coexistence: a non-equilibrium model. *American Naturalist* 112:127–154.
- Caswell, H., and J. E. Cohen. 1991. Disturbance, interspecific interaction and diversity in metapopulations. *Biological Journal of the Linnean Society* 42:193–218.
- Cochran-Stafira, D. L., and C. N. von Ende. 1998. Integrating bacteria into food webs: studies with *Sarracenia purpurea* inquilines. *Ecology* 79:880–898.
- Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist* 137:1–26.
- Forbes, A. E., and J. M. Chase. 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. *Oikos* 96:433–440.
- Gilbert, F., A. Gonzalez, and I. Evans-Freke. 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. *Proceedings of the Royal Society of London B, Biological Sciences* 265:577–582.
- Gonzalez, A., J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* (Washington, D.C.) 281:2045–2047.
- Gotelli, N. J., and G. L. Entsminger. 2001. EcoSim: null models software for ecology. Version 6.0. Acquired Intelligence, Kesey-Bear. <http://homepages.together.net/~gentsmin/ecosim.htm>.
- Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution, Washington, D.C.
- Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford.
- Harvey, E., and T. E. Miller. 1996. Variance in composition of inquiline communities in leaves of *Sarracenia purpurea* L. on multiple spatial scales. *Oecologia* (Berlin) 108:562–566.
- Heard, S. B. 1994. Imperfect oviposition decisions by the pitcher plant mosquito (*Wyeomyia smithii*). *Evolutionary Ecology* 8:493–502.
- Holyoak, M., and S. P. Lawler. 1996. The role of dispersal in predator-prey metapopulation dynamics. *Journal of Animal Ecology* 65:640–652.
- Horn, H. S., and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. *Ecology* 53:749–752.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27:343–383.
- Istock, C. A., S. S. Wasserman, and H. Zimmer. 1975. Ecology and evolution of the pitcher plant mosquito. I. population dynamics and laboratory responses to food and population density. *Evolution* 29:296–312.
- Kneitel, J. M. 2002. Species diversity and trade-offs in *Sarracenia purpurea* inquiline communities. Ph.D. diss. Florida State University.
- Kneitel, J. M., and T. E. Miller. 2002. Resource and top-predator regulation in the pitcher plant (*Sarracenia purpurea*) inquiline community. *Ecology* 83:680–688.
- Lawler, S. P., and P. J. Morin. 1993. Food web architecture and population dynamics in laboratory microcosms of protists. *American Naturalist* 141:675–686.
- Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* 147:784–812.
- Levin, S. A. 1974. Dispersion and population interactions. *American Naturalist* 108:207–228.
- Loreau, M., and N. Mouquet. 1999. Immigration and the maintenance of local species diversity. *American Naturalist* 154:427–440.
- Luckinbill, L. S. 1979. Regulation, stability, and diversity in a model experimental microcosm. *Ecology* 60: 1098–1102.
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of

- island biogeography. Princeton University Press, Princeton, N.J.
- Maguire, B., Jr. 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. *Ecological Monographs* 33:161–185.
- Miller, T., D. Cassill, C. Johnson, C. Kindell, J. Leips, D. McInnes, T. Bevis, D. Mehlman, and B. Richard. 1994. Intraspecific and interspecific competition of *Wyeomyia smithii* (Coq.) (Culicidae) in pitcher plant communities. *American Midland Naturalist* 131:136–145.
- Miller, T. E., J. M. Kneitel, and J. H. Burns. 2002. Effect of community structure on invasion success and rate. *Ecology* 83:898–905.
- Mouquet, N., and M. Loreau. 2002. Coexistence in metacommunities: the regional similarity hypothesis. *American Naturalist* 159:420–426.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Patterson, D. J. 1996. Free-living freshwater protozoa. Wiley, New York.
- Pennak, R. W. 1989. Freshwater invertebrates of the United States. Wiley, New York.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Revill, D. L., K. W. Stewart, and H. E. Schlichting. 1967. Passive dispersal of viable algae and protozoa by certain craneflies and midges. *Ecology* 48:1023–1027.
- Shmida, A., and M. V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12: 1–20.
- Shorrocks, B. 1991. Competition on a divided and ephemeral resource: a cage experiment. *Biological Journal of the Linnean Society* 43:211–220.
- Shurin, J. B. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* 81:3074–3086.
- . 2001. Interactive effects of predation and dispersal on zooplankton communities. *Ecology* 82:3404–3416.
- Shurin, J. B., and E. G. Allen. 2001. Effects of competition, predation and dispersal on local and regional species richness. *American Naturalist* 158:624–637.
- Simberloff, D. S., and E. O. Wilson. 1970. Experimental zoogeography of islands: a two-year record of colonization. *Ecology* 51:934–937.
- Taylor, A. D. 1988. Large-scale spatial structure and population dynamics in arthropod predator-prey systems. *Annale Zoologici Fennici* 25:63–74.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, N.J.
- Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittlebach, L. Gough, S. I. Dodson, G. P. Juday, and R. Pamerter. 1999. The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* 30: 257–300.
- Warren, P. H. 1996a. Dispersal and destruction in a multiple habitat system: an experimental approach using protist communities. *Oikos* 77:317–325.
- . 1996b. The effects of between-habitat dispersal rate on protist communities and metacommunities in microcosms at two spatial scales. *Oecologia (Berlin)* 105: 132–140.
- Zar, J. H. 1996. Biostatistical analysis. Prentice Hall, Upper Saddle River, N.J.