

EFFECT OF COMMUNITY STRUCTURE ON INVASION SUCCESS AND RATE

THOMAS E. MILLER,¹ JAMIE M. KNEITEL, AND JEAN H. BURNS

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

Abstract. Although invasion has long been recognized as an important ecological process, there are very few experimental studies of invasion in natural communities and virtually no studies that determine how trophic structure affects the probability of invasion. We introduced novel protozoans and rotifers into the natural communities found in the water-filled leaves of the pitcher plant *Sarracenia purpurea*. The communities were manipulated in a factorial design of removal of predators (larvae of the mosquito *Wyeomyia smithii*) and addition of resources (dead insects). Three of the six protozoan species successfully established populations when introduced into pitchers, suggesting that these species are migration limited. The other three protozoans and a rotifer did not successfully invade established communities, although all four are naturally found in these inquiline communities. Of the three successfully invading protozoans, two were more likely to invade when resources were added and one of those even more frequently when predators were removed. Invasion by the third was unaffected by these experimental manipulations. Similar effects of predators and resources were found on population sizes of these three species. This study is one of very few that have addressed invasion experimentally; its results suggest that a variety of factors, including migration, predation, and resource availability, can have different influences on invasion by fairly similar protozoans.

Key words: aquatic community invasion, manipulative study of; community structure affects invasion success; *Habrotrocha rosa*; invasion success, factors affecting; predation; Protozoa; resource levels; *Sarracenia purpurea*; *Wyeomyia smithii*.

INTRODUCTION

Invasion by alien species has increasingly been recognized as one of the major worldwide environmental problems of the last century. "Invasion," or migration of new species into local communities, can also be important for community development (e.g., succession, Connell and Slatyer 1977) and for community structure and composition (MacArthur and Wilson 1967, Ricklefs and Schluter 1993, Loreau and Mouquet 1999). Ecologists know remarkably little, however, about what factors facilitate or prevent invasion, in part because of the dearth and difficulty of experimental studies.

Most of our current knowledge of this process comes from either observational or theoretical studies. Observational studies have focused on identifying traits that are common to successful invasive species (Newsome and Noble 1986, Noble 1989, Perrins et al. 1992, Veltman et al. 1996). It has frequently been assumed, for example, that successful invasive species will have traits of "weedy" species (Baker 1974), such as rapid growth to reproductive age, high offspring production, and potential long-distance dispersal of propagules. It has proven difficult, however, to categorize successful invasive species by any unique set of traits (see, e.g., Newsome and Noble 1986, Lonsdale 1994).

Manuscript received 14 September 2000; revised 10 July 2001; accepted 13 July 2001.

¹ E-mail: miller@bio.fsu.edu

Theoretical approaches have emphasized traits of communities that affect the probability of invasion, rather than traits of invasive species. This work has largely developed from Elton's suggestion that resistance to invasion is correlated with species number (Elton 1958, Levine and D'Antonio 1999), an idea that is certainly consistent with, if not drawn from, the niche concept. Several theoretical models have proposed a negative relationship between the probability of successful invasion and species richness or between the probability of successful invasion and the intensity of species interactions (Case 1990, 1991, Cornell and Lawton 1992, Morton and Law 1997). In these models, the dominant force limiting invasion is competition for resource niches, and current occupants are generally viewed as having a competitive advantage. Successful invaders must generally displace current species or use empty or underused niches.

Although several studies have investigated invasion using laboratory microcosms (e.g., Robinson and Dickerson 1984), very few studies have used controlled experimental introductions of species into natural communities (see Levins and Heatwole 1973). Several studies have investigated the effects of native species richness on invasion of natural communities, with contradictory results. Whereas some studies found that species richness decreased the probability of successful invasion (e.g., Tilman 1997, Stachowicz et al. 1999), others found no effect of richness (e.g., Peart and Foin

1985) or even a positive effect of species richness on invasion (e.g., Robinson et al. 1995).

The effects of resource levels on invasion have also been studied. Burke and Grime (1996) studied invasion over gradients of soil disturbance and fertilizer application and found that fertilizer did increase the biomass of invasive species, although only at higher levels of soil disturbance. A similar pattern was found by Huenneke et al. (1990), who manipulated nutrient availability in serpentine grasslands and observed the influence on invasion.

Virtually no experimental evidence addresses how predators, rather than competitors, affect the probability of successful invasion by potential prey (see Levins and Heatwole 1973, Baltz and Moyle 1993, Schoener and Spiller 1995). Classic ecological theory suggests that predators could have two opposite effects on the invading species. Direct predation could result in negative effects of predators on invaders, preventing or slowing the rate of invasion. On the other hand, indirect effects (e.g., keystone predation) could result in positive effects of predation on invasiveness (Holt 1977). We know of a single manipulative study on this subject: lizard predators were found to impede the establishment of spiders on islands (Schoener and Spiller 1995).

We have manipulated both the presence of predators and levels of resources (dead insects) in the small aquatic communities found in the leaves of the carnivorous pitcher plant *Sarracenia purpurea* L. We then introduced novel pitcher-plant protozoans into these communities and quantified their success as a function of community structure to determine whether the occurrence of these species was limited by migration. Where species were successfully established, we quantified the effects of predation and resource availability on invasion probability and invader abundance. A strength of this experimental approach is that it quantifies effects of both trophic structure (the presence of predators) and habitat characteristics (resource levels), as well as their interaction, on invasion success.

MATERIALS AND METHODS

Our experiments were conducted in a bog located in a large savanna surrounded by longleaf pine forest 3 km north of Sumatra, Florida, USA. The field contains hundreds of *Sarracenia purpurea* individuals, in a mixed grassland with *Aristida stricta* and a number of other insectivorous species, including *S. flava*, *S. psitticina*, *Drosera capillaris*, and several *Pinguicula* species. Individuals of *S. purpurea* generally have 3–12 cup-shaped leaves, each of which holds up to 50 mL of rainwater and serves as a trap that captures a number of different invertebrates, including ants, worms, and spiders. These prey are thought to provide important nutrients for the plant in nutrient-poor bogs.

The inquiline community found in *S. purpurea* leaves has been described elsewhere (Addicott 1974, Harvey and Miller 1996, Cochran-Stafira and von Ende

1998) and will be described only briefly here. In northern Florida, it frequently includes larvae from two dipterans, the mosquito *Wyeomyia smithii* and the chironomid *Metriocnemus knabi*, both obligate pitcher-plant inquilines. *Metriocnemus knabi* feeds directly on drowned prey captured by the leaf (Heard 1994), whereas *W. smithii* is a filter-feeder, thought to feed on rotifers, protozoans, and possibly bacteria. The bdelloid rotifer *Habrotrocha rosa* (Bateman 1987) can be very abundant in pitchers and has been shown to be important for nutrient dynamics within pitcher communities (Bledzki and Ellison 1998). Histiostomatid mites, *Sarraceniopus gibsoni* (Nesbitt), are also frequent residents in many pitchers (Fashing and O'Connor 1984), as are occasional copepods and cladocerans. Less is known about the protozoans and bacteria found in *S. purpurea* (Prankevicius and Cameron 1989, 1991), although these species clearly make up the resource base for higher trophic levels in the community (Cochran-Stafira and von Ende 1998, Kneitel and Miller 2002). Both protozoans (L. Gensel and T. E. Miller, *unpublished manuscript*) and bacteria (Harvey and Miller 1996) are nonrandomly distributed among pitchers, presumably because of strong species interactions.

The ambient abundances of the species in this study can be highly variable (Harvey and Miller 1996); values noted here are from personal observation from the spring of 1999. Mosquito-larva densities averaged 5.0 individuals per pitcher, but other dipteran larvae were largely absent until early summer. Pitcher volume depended on recent rainfall and ranged from 2 to 18 mL (mean 8.0 mL). Protozoan densities can vary with species, but total densities averaged 90 individuals/mL. Rotifers can be equally abundant, at 111 individuals/mL. Bacterial abundance was also variable, commonly in the range of 10^5 – 10^7 cells/mL. Prey found in northern Florida pitchers included ants (mostly *Solenopsis invicta*), along with a variety of spiders and other invertebrates.

The mechanism by which protozoans and rotifers migrate naturally among communities is unknown, but they are generally thought to have high potential for dispersal (Maguire 1977). Harvey and Miller (1996) found greater similarity in bacterial community composition among leaves on the same plant than among leaves on different plants, consistent with decreasing migration with increasing distance. Potential mechanisms for such dispersal may include splashing from nearby pitchers during rainstorms, droplets of water carried on insects or other organisms that may move from pitcher to pitcher (Maguire 1963, Revill et al. 1967, Schlichting and Sides 1969), and cysts dispersed by the wind.

We manipulated communities in the field by varying the abundance of the top predator, *W. smithii*, and the abundance of basal resources for the community, invertebrate prey of the pitcher plant. These communities

TABLE 1. Protozoan species and rotifers used in each inoculation of field *Sarracenia purpurea* leaves, along with their feeding behavior and abundance in the inoculate used to colonize pitcher-plant communities.

Invader	Taxonomic group	Feeding behavior	Abundance (no. individuals/drop) [†]
Protozoa			
<i>Bodo</i>	family Bodonidae	suspension	2345 ± 535
Chryomonad	class Chryomonadea	suspension	990 ± 282
<i>Cyclidium</i>	family Cyclidiidae	suspension	10 ± 13
<i>Colpidium</i>	family Turaniellidae	suspension, grazer	10 ± 13
<i>Colpoda</i>	family Colopodidae	suspension, grazer	102 ± 47
Species A	unknown	suspension	102 ± 52
Rotifers			
<i>Habrotrocha rosa</i>	family Bdelloidea	suspension, grazer	35 ± 52

[†] Abundance data are means ± 1 SE; one drop = ~0.05 mL.

were then inoculated with a mixed assemblage of protozoans. The experimental design was factorial, including two levels of mosquitoes (0 and 5 individuals per pitcher), two levels of resources (no addition and addition of 1/2 a sterilized mealworm), and two inoculation states (inoculated and control) in 6 blocks with one replicate per block ($2 \times 2 \times 2 \times 6 = 48$ communities). Treatments were implemented in healthy, water-filled leaves of separate plants and were randomly assigned to leaves within blocks. From setting up of the treatments through the end of the experiment, except during actual sampling, all pitchers were covered with white bridal-veil material to minimize uncontrolled arrival of mosquitoes or prey.

The assemblage of species used for inoculation in this study was obtained from several pitcher plants that had been transplanted from the Sumatra area to outdoor pools in Tallahassee, Florida, two years earlier. These plants harbored protozoan species and rotifers typically found in natural inquiline communities, albeit at somewhat higher densities. The high abundances may be related to the loss of mosquitoes from these transplanted populations. The protozoan species have been tentatively identified to genus, where possible (Table 1), according to Patterson (1996). These species are known also to occur in the Pleaphase Savanna, although they are relatively rare in mid-spring, when this experiment was initiated. Virtually all of these species are bacteriovores that feed on suspended material, although some may also graze on attached bacteria (*Colpidium*, *Colpoda*, *H. rosa*).

We inoculated pitchers by transferring ~0.05 mL (one drop) of this assemblage into appropriate leaves at the beginning of the experiment and then followed the subsequent abundances of these species in all pitchers. This artificial dispersal mimics splashing from nearby pitchers or the movement of droplets by animal vectors. To determine the numbers of individuals being transferred by this method, we censused three replicate drops (Table 1). The abundances of the transferred species varied by two orders of magnitude, but each drop should contain representatives of six protozoan species

and the rotifer, *H. rosa*. The small chance that some of the rare species were not transferred into all pitchers would have been independent of treatment.

One-half of the communities were inoculated on 6 April 2000; then all communities were sampled 2, 4, 6, 10, and 14 d later, which conservatively represents over 50 generations for protozoan population growth. Before inoculation and at each subsequent sampling date, the entire fluid contents of the pitcher were gently mixed, removed with a sterile pipette, and censused for mosquitoes. We adjusted mosquito abundances where necessary at each sampling date by removing extra individuals. A small amount of the mixed fluid (~1 mL) was reserved from each pitcher and returned to the laboratory to be censused for protozoans and rotifers. The remaining fluid was then replaced in the original pitcher, and the bridal veil cover was replaced. At final sampling, the entire contents of the pitchers were removed and censused for mosquitoes, cladocerans, mites, rotifers, and protozoans. Censuses for protozoans and rotifers were conducted with a hemacytometer under a microscope at 125 \times . Two counts were taken for each sample, then summed. Bacterial abundance was determined on the final census date. Fluid from each community was serially diluted to 10³ and 10⁵ with a saline buffer. Luria agar plates were then used to plate 0.1 mL from each dilution, and all bacterial colonies were counted after 72 h of incubation at 26°C.

Because the data are right censored, the Kaplan Meier Survival platform of the statistical discovery software JMP (SAS Institute 1996) was used to determine the inoculation success of each species. In this analysis, a community "survives" if it remains uninhabited by species from the inoculum, and the "survival" patterns (numbers of uninhabited communities) through time of different treatments can be compared. The survival functions were generally best fit by a Weibull distribution, although other distributions and non-parametric product-moment methods gave similar results. On the assumption of the Weibull distribution, the inoculated and control communities were compared

by means of an iterative maximum-likelihood regression, and the likelihood ratio was evaluated by means of a chi-square statistic. If a species was shown to invade the pitcher communities successfully, then a second model, using data only from the pitchers that were inoculated, was applied to test the effects of mosquitoes, prey addition, and their interaction on the probability of invasion. The effects of mosquitoes and prey on the abundances of the successful invaders through time were tested with repeated-measures ANOVA (SAS Institute 1990) on log-transformed abundances of protozoan species that successfully invaded the experimental communities. In all tests, the assumption of compound symmetry was rejected (Mauchley's test, $P < 0.001$), so a Hunyh-Feldt test was used to determine whether the symmetry assumption could be relaxed (Potvin et al. 1990). Violation with *Bodo* results was mild, but the chryomonad and *Cyclidium* results should be interpreted with caution. The effects of treatments on log-transformed bacterial abundances from the final census were evaluated by a two-way ANOVA with main effects of mosquitoes, prey addition, and their interaction.

RESULTS

Most of the pitcher plants used in this study remained healthy during the period of the experiment, developing flower buds and beginning to produce new leaves. A single control community was damaged during sampling on day 10 and was deleted from subsequent analyses. Of the potential invading species, all but Species A appeared in low abundances in control pitchers during the course of the experiment; because these species are unlikely to have come from our covered-treatment pitchers, their appearance in controls confirms that they occur normally in this habitat.

Three of the six protozoan species in our inoculate successfully invaded communities: *Bodo*, the chryomonad, and *Cyclidium* were all found significantly more frequently in inoculated than in control pitchers

(Table 2). *Bodo* was the most successful invader (Fig. 1A), appearing in 10 of the 24 inoculated pitchers two days after inoculation (as opposed to 1 of 24 control pitchers). By the end of the experiment, *Bodo* had become established in 19 of the 24 communities. In contrast, the chryomonad and *Cyclidium* had become established in 11 and 6 communities, respectively, after 14 d (Fig. 1B and C, respectively). *Colpidium*, *Colpoda*, and the rotifer, *Habrotrocha rosa*, were found in a limited number of the experimental pitchers, but their occurrence was not a function of the inoculation treatment (Table 2). Species A was never found during the course of the experiment.

The effects of mosquitoes and resource additions on the establishment of *Bodo*, the chryomonad, and *Cyclidium* were quantified on the basis of data from the inoculated communities only. The number of communities successfully invaded by *Bodo* was higher both when mosquitoes were absent and when resources were added (Table 2, Fig. 1A); no significant interaction was apparent between mosquitoes and resources. Chryomonad invasion was only marginally significantly higher when resources were increased and was unaffected by mosquitoes (Table 2, Fig. 1B). The rate of *Cyclidium* invasion was not affected by mosquitoes or resources (Table 2, Fig. 1C).

Abundances of the successful invaders were also found to vary with treatment. As with invasion probability, *Bodo* abundances were higher in the absence of mosquitoes and the presence of added resources (Table 3, Fig. 2A), but the effects of mosquitoes and resources appear less than additive, as indicated by the marginally significant interaction term ($P = 0.058$). Chryomonad abundance was marginally higher with resource addition but was not affected by mosquito removal (Table 3, Fig. 2B). *Cyclidium* abundance was not affected by resource addition or by mosquitoes (Table 3, Fig. 2C).

Bacterial abundance was significantly greater when mosquito predators were present ($F = 4.16, P = 0.04,$

TABLE 2. Results of survival analyses testing for invasion success in pitcher-plant communities.

Invader	P	P values, effects of treatments		
		Predators (P)	Resources (R)	P × R
Protozoa				
<i>Bodo</i>	<0.001 (21.74)	<0.017 (5.73)	<0.018 (5.68)	0.88 (0.06)
Chryomonad	<0.05 (3.88)	0.56 (0.34)	0.08 (3.01)	0.56 (0.34)
<i>Cyclidium</i>	<0.031 (4.66)	0.41 (0.67)	0.44 (0.57)	0.41 (0.67)
<i>Colpidium</i>	0.94 (0.01)
<i>Colpoda</i>	0.12 (2.41)
Species A	0.15 (2.04)
Rotifers				
<i>Habrotrocha rosa</i>	0.39 (0.75)

Notes: If a species could invade successfully, in tests comparing inoculated and uninoculated communities, then only inoculated communities were used in tests for the effects of predators, resources, and their interaction. Chi-square values used to determine the significance of the likelihood ratio are given in parentheses. Ellipses indicate analyses were not conducted.

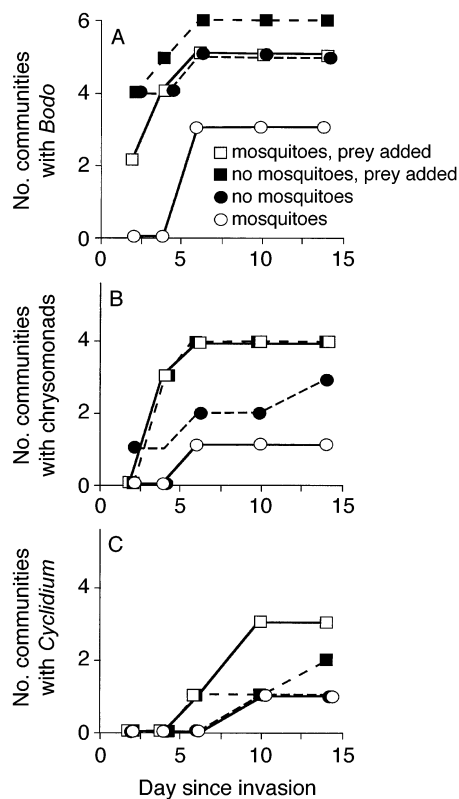


FIG. 1. Numbers of successfully invaded communities through time for three protozoans: (A) *Bodo* sp., (B) the chryomonad, and (C) *Cyclidium* in manipulated pitcher-plant leaves in the Pleiophase Savanna near Sumatra, Florida, USA. Treatments: solid squares = mosquito predators removed and prey added; solid circles = only mosquito predators removed; open squares = only prey added; open circles = control communities. The control community included only mosquitoes.

df = 1; Fig. 3) but was not significantly affected by the addition of prey ($F = 2.35$, $P = 0.13$, df = 1). The effects of predators and resources did not interact significantly ($F = 0.513$, $P = 0.48$, df = 1).

DISCUSSION

We conclude that the distributions of three of the protozoan species we introduced into the aquatic communities in pitcher-plant leaves are limited by dispersal. Distribution of the remaining three protozoans and the rotifer species are affected by other factors not manipulated in this experiment. The successfully invading species established large populations after relatively few individuals were experimentally introduced. Clearly, successful invasion in this experiment involved population growth within pitchers and not rescue effects (Brown and Kodric-Brown 1977) or "sink" dynamics (Holt 1993, Loreau and Mouquet 1999).

Invasion success in the pitcher-plant communities depended on resource availability, predator presence, and the identity of the potential invader. Frequency of invasion by *Bodo* and the chryomonad was increased by addition of dead prey to the pitchers. The increased invasion success of protozoa may be due to the increased bacterial abundances that are known to occur when dead prey are added to pitchers (Kneitel and Miller 2002); similar effects of resource addition on invasibility have been demonstrated in terrestrial plant communities (Huenneke et al. 1990, Burke and Grime 1996). Although bacterial densities tended to be higher when resources were added, we found no significant effect of resource addition on bacterial abundance on day 14 (Fig. 3). Although bacterial productivity may be increased, the correlated increase in protozoans and

TABLE 3. Results of repeated-measures ANOVA on protozoan abundance over time.

Dependent variable	Level	Source of variation	df	F	P
<i>Bodo</i>	Between subjects	Predator, P	1	4.24	0.053
		Resource, R	1	9.92	0.005
		P × R	1	4.03	0.058
		Error	20		
	Within subjects	P × Time (T)	5	24.96	0.300
		R × T	5	4.49	0.004
P × R × T		5	1.77	0.151	
Chryomonad	Between subjects	Predator	1	1.41	0.249
		Resource	1	3.60	0.073
		P × R	1	1.42	0.247
		Error	20		
	Within subjects	P × T	5	1.27	0.28
		R × T	5	2.02	0.16
P × R × T		5	1.28	0.28	
<i>Cyclidium</i>	Between subjects	Predator	1	1.15	0.297
		Resource	1	0.01	0.920
		P × R	1	0.37	0.547
		Error	20		
	Within subjects	P × T	5	0.32	0.71
		R × T	5	0.67	0.51
P × R × T		5	1.64	0.21	

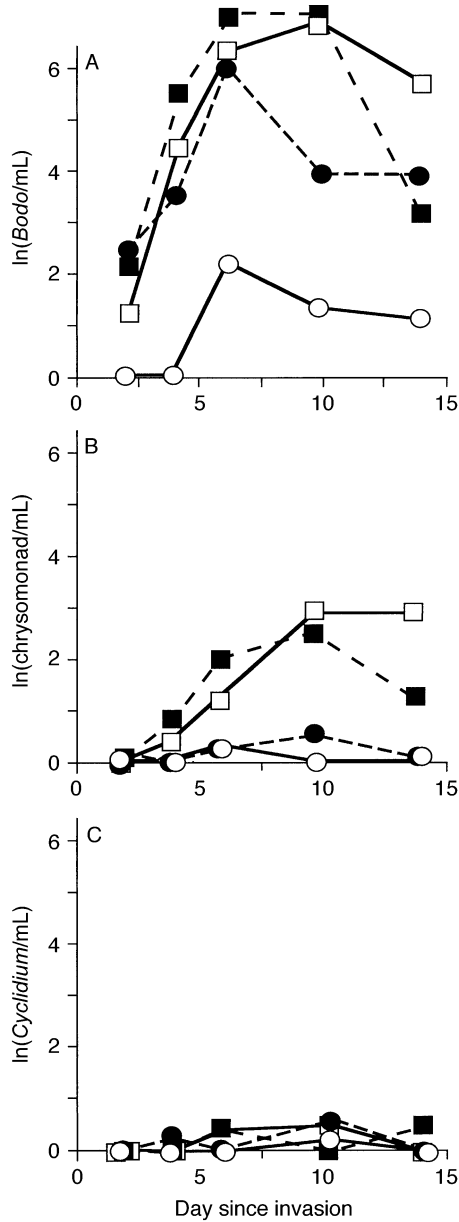


FIG. 2. Densities of three successfully invading protozoans: (A) *Bodo* sp., (B) the chryomonad, and (C) *Cyclidium* through time in manipulated pitcher-plant leaves in the Plea-phase Savanna near Sumatra, Florida, USA. Treatments are as in Fig. 1.

rotifers may keep standing abundances of bacteria low (Kneitel and Miller 2002).

Further, the invasion success of *Bodo* was also increased by the removal of predatory larvae of the mosquito *Wyeomyia smithii*. Mosquito larvae are generalist feeders that have been shown to affect protozoan abundances in pitcher communities (Addicott 1974, Cochran-Stafira and von Ende 1998). The presence of predators did result in an increase in bacterial abundance (Fig. 3), which may arise from a trophic cascade that

results when mosquitoes reduce the abundance of protozoans. The third successful invader was apparently limited by migration; manipulation of predators and resources had no effect on the invasion success of *Cyclidium*. Therefore, successful invasion sometimes depends on characteristics of the habitat, consistent with theoretical predictions of invasibility based on habitat characteristics (e.g., Case 1991), and sometimes depends only on characteristics of the invading species, as observational studies have suggested (e.g., Noble 1989).

Initial density of species in the inoculum may affect invasion success. *Bodo* and the chryomonad, the most abundant species in the inoculum, were the most successful invaders, but *Cyclidium*, the third successful invader, was relatively rare in the inoculum.

The source of the invaders may also affect invasion success. In this case, all the potential protozoan and rotifer invaders were species that had previously been found in this bog. The source communities for the inoculum, transplanted pitchers in outdoor pools in Tallahassee (Florida, USA), lost their mosquito populations soon after they were moved to Tallahassee. This loss of a major predator of protozoans may be what now allows high protozoan and rotifer densities.

Interactions in pitcher-plant leaves occur at two distinct scales. At the local, within-leaf scale, species interactions such as competition and predation may strongly affect local diversity and the relative abundance of species. At the among-leaf, or regional, scale individual leaves represent long-term habitats relative to the generation times of the inquiline organisms, but eventually all leaves die. Component species must

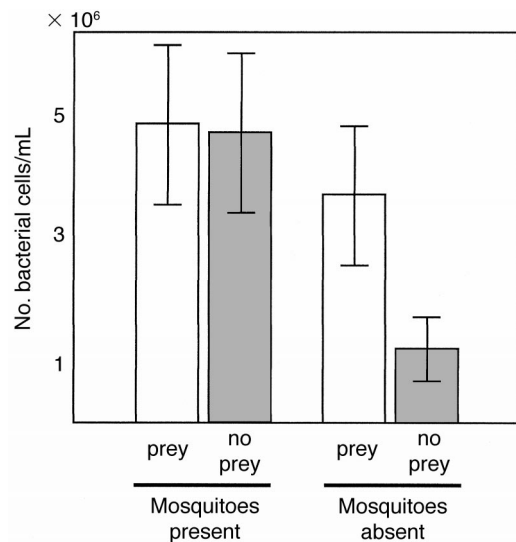


FIG. 3. Effect of treatments on bacterial abundance. Bacteria were sampled on day 14 of the experiment. The numbers of bacterial cells are estimates of cell abundance from colony growth on agar plates following serial dilutions. Data are means \pm 1 SE.

therefore be able to disperse among these ephemeral habitats, and migration must also play a role in determining both local and regional patterns of diversity. The species in our study demonstrate the importance of both local and regional processes and the distinction between them. This result is consistent with the findings of both Stohlgren et al. (1999) and Levine (2000), who suggest that processes at different spatial scales can have significant and very different effects on invasion processes. The ability of organisms like *Bodo* and the chryomonad to colonize new leaves is limited both by their ability to disperse and by local processes related to predation and the availability of resources. In contrast, *Cyclidium* was limited only by dispersal; it was apparently unaffected by our manipulations of local species interactions. Local and regional processes thus vary in importance, depending in part on individual species characteristics. The factors limiting the three other protozoans and the rotifer, *Habrotrocha rosa*, were not revealed by the present study. Clearly, these species are not solely limited by migration, but may be limited by uninvestigated local factors such as the presence of particular prey species or levels of prey abundance.

The present study is one of the first manipulative studies of invasion in aquatic communities and one of the first to manipulate directly the presence of natural predators simultaneously with the abundance of resources. The different limiting factors and effects of scale for different species that we demonstrate are consistent with our general theoretical understanding of metacommunity dynamics. Both local and regional factors are expected to limit species abundances and distributions, and these factors are expected to differ in relative importance for different species. Species easily suppressed by competitors or predators may persist through continuous and widespread dispersal to new habitats (Hutchinson 1961, Levins and Culver 1971, Caswell 1978). Such species will be greatly affected by species interactions at the local scale. Other species, which dominate in local species interactions, may be limited by the ability to disperse to new habitats. The present study can also be interpreted in light of "assembly rules" (see, e.g., Drake 1991, Weiher and Keddy 1999), in that the current composition of the community can affect later successional patterns.

The probability of successful invasion therefore depends on local characteristics like resource availability and species interactions, regional processes like dispersal, and the characteristics of potential invaders. Other factors may also be important for determining invasion success, such as the timing (see, e.g., Martins and Jain 1979) or number of invasions (Veltman et al. 1996, Loreau and Mouquet 1999). Our next step is to determine how the balance among these factors determines patterns of diversity at different scales, from local to regional, and to attempt further elucidation of the biological mechanisms behind these patterns.

ACKNOWLEDGMENTS

We are grateful for advice from R. Reeves, J. Reeves, and D. L. Cochran-Stafira. Comments of three reviewers have greatly improved the manuscript. This research was partially supported by NSF grants DEB 0083617 and DEB 0091776 to T. E. Miller.

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.
- Baker, H. G. 1974. The evolution of weeds. *Annual Review of Ecology and Systematics* **5**:1–24.
- Baltz, D. M., and P. B. Moyle. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecological Applications* **3**:246–255.
- Bateman, L. E. 1987. A bdelloid rotifer living as an inquiline in leaves of the pitcher plant, *Sarracenia purpurea*. *Hydrobiologia* **147**:129–133.
- 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., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**:445–449.
- Burke, J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* **77**:776–790.
- Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences (USA)* **87**:9610–9614.
- Case, T. 1991. Invasion resistance, species build-up and community collapse in metapopulation models with interspecific competition. *Biological Journal of the Linnean Society* **42**:239–266.
- Caswell, H. 1978. Predator-mediated coexistence: a non-equilibrium model. *American Naturalist* **122**:127–154.
- Cochran-Stafira, D. L., and C. N. von Ende. 1998. Integrating bacteria into food webs: studies with *Sarracenia purpurea* inquilines. *Ecology* **79**:880–898.
- Cornell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**:1119–1144.
- Cornell, H. V., and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* **61**:1–12.
- Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist* **137**:1–26.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London, UK.
- Fashing, N. J., and B. M. O'Connor. 1984. *Sarraceniopus*—a new genus for histiostomatid mites inhabiting the pitchers of Sarraceniaceae (Astigmata: Histiostomatidae). *International Journal of Acarology* **10**:217–227.
- Harvey, E., and T. E. Miller. 1996. Variance in composition of inquiline communities in leaves of *Sarracenia purpurea* L. on multiple spatial scales. *Oecologia* **108**:562–566.
- Heard, S. B. 1994. Pitcher-plant midges and mosquitoes: a processing chain commensalism. *Ecology* **75**:1647–1660.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* **12**:197–229.
- Holt, R. D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. Pages 77–88 in

- R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois, USA.
- Huenneke, L. F., F. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* **71**:478–491.
- Hutchinson, G. E. 1961. The paradox of the plankton. *American Naturalist* **95**:137–145.
- Kneitel, J. M., and T. E. Miller. 2002. The effects of resource and top-predator addition to the inquiline community of the pitcher plant *Sarracenia purpurea*. *Ecology* **83**:680–688.
- Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* **288**:852–854.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**:15–26.
- Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences (USA)* **68**:1246–1248.
- Levins, R., and H. Heatwole. 1973. Biogeography of the Puerto Rican Bank: introduction of species onto Palominitos Island. *Ecology* **54**:1056–1064.
- Lonsdale, W. M. 1994. Inviting trouble: introduced pasture species in northern Australia. *Australian Journal of Ecology* **19**:345–354.
- Loreau, M., and N. Mouquet. 1999. Immigration and the maintenance of local species diversity. *American Naturalist* **154**:427–440.
- MacArthur, R., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Maguire, B., Jr. 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. *Ecological Monographs* **33**:161–185.
- Maguire, B., Jr. 1977. Community structure of protozoans and algae with particular emphasis on recently colonized bodies of water. Pages 355–397 in J. Cairns, Jr., editor. *Aquatic microbial communities*. Garland, New York, New York, USA.
- Martins, P. S., and S. K. Jain. 1979. Role of genetic variation in the colonizing ability of rose clover (*Trifolium hirtum* All.). *American Naturalist* **114**:591–595.
- Morton, R. D., and R. Law. 1997. Regional species pools and the assembly of local ecological communities. *Journal of Theoretical Biology* **187**:321–331.
- Newsome, A. E., and I. R. Noble. 1986. Ecological and physiological characters of invading species. Pages 1–20 in R. H. Groves and J. J. Burdon, editors. *Ecology of biological invasions*. Cambridge University Press, Cambridge, UK.
- Noble, I. R. 1989. Attributes of invaders and the invading process: terrestrial and vascular plants. Pages 301–313 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. *Biological invasions: a global perspective*. John Wiley and Sons, Chichester, UK.
- Patterson, D. J. 1996. Free-living freshwater protozoa. John Wiley and Sons, New York, New York, USA.
- Peart, D. R., and T. C. Foin. 1985. Analysis and prediction of community change: a grassland case study. Pages 312–339 in J. White, editor. *The population structure of vegetation*. Junk, Dordrecht, The Netherlands.
- Perrins, J., M. Williamson, and A. Fitter. 1992. Do annual weeds have predictable characters? *Acta Oecologia* **13**:517–533.
- Potvin, C., M. L. Lechowicz, and S. Tardif. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology* **71**:1389–1400.
- Prankevicus, A. B., and D. M. Cameron. 1989. Free-living dinitrogen-fixing bacteria in the leaf of the northern pitcher plant (*Sarracenia purpurea* L.). *Naturaliste Canadien (Québec)* **116**:245–249.
- Prankevicus, A. B., and D. M. Cameron. 1991. Bacterial dinitrogen fixation in the leaf of the northern pitcher plant (*Sarracenia purpurea*). *Canadian Journal of Botany* **69**:2296–2298.
- Revell, D. L., K. W. Stewart, and H. E. Schlichting, Jr. 1967. Passive dispersal of viable algae and protozoa by certain craneflies and midges. *Ecology* **48**:1023–1027.
- Ricklefs, R. E., and D. Schluter. 1993. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois, USA.
- Robinson, G. R., J. F. Quinn, and M. L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* **76**:786–794.
- Robinson, J. V., and J. E. Dickerson. 1984. Testing the invulnerability of laboratory island communities to invasion. *Oecologia* **61**:169–174.
- SAS Institute. 1990. SAS/STAT user's guide. Version 6, fourth edition. SAS Institute, Cary, North Carolina, USA.
- SAS Institute. 1996. JMP IN. Version 3.2. SAS Institute, Cary, North Carolina, USA.
- Schlichting, H. E., Jr., and S. L. Sides. 1969. The passive transport of aquatic microorganisms by selected Hemiptera. *Journal of Ecology* **57**:759–764.
- Schoener, T. W., and D. A. Spiller. 1995. Effects of predators and area on invasion: an experiment with island spiders. *Science* **267**:1811–1813.
- Stachowicz, J. J., R. B. Whitlatch, and R. W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. *Science* **286**:1577–1579.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* **69**:25–46.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**:81–92.
- Veltman, C. J., S. Nee, and M. J. Crawley. 1996. Correlates of introduction success in exotic New Zealand birds. *American Naturalist* **147**:542–557.
- Weiherr, E., and P. Keddy. 1999. Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, Cambridge, UK.