



Trophic interactions in the phytotelmata communities of the Pitcher Plant, *Sarracenia purpurea*

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Abstract: A pulse-perturbation experiment, designed to assess the impact of top predators, resource availability, and the interaction between predators and resources, was conducted in the inquiline community found in a natural population of the pitcher plant *Sarracenia purpurea*. Experimental manipulations of pitchers were removal of the top predator (the filter-feeding larvae of the mosquito *Wyeomia smithii*), addition of resources (mealworms), and the combination of the two. Pitchers were then censused every three days for 15 days. Top-predator removal had little effect on the remaining community, in part because mosquitoes rapidly recolonized the pitchers. Resource addition resulted in large, persistent increases in both bacterial and protozoan abundances but had no effect on rotifers and mites. Therefore, "top-down" effects were relatively weak. In contrast, "bottom-up" effects were strong at the lowest trophic level (bacteria) but differentially affected species at a higher trophic level that feed on bacteria. The interactions between top-down and bottom-up forces were difficult to quantify because of the rapid recolonization by mosquitoes.

Abbreviation: ANOVA - Analysis of Variance.

Introduction

Perhaps the biggest obstacle to our understanding natural communities is complexity. A simplified view of communities, primarily based on niche theory, has provided some useful generalizations but does not adequately explain the variation observed among real communities. Even though relatively simple models of certain multispecies assemblages, such as the intermediate disturbance principle, apparent competition, and indirect effects (Menge 1995), have led to our appreciation of the potential for multispecies interactions, community ecology is far from a predictive science. We have a poor grasp of when generalized principles apply or how they are affected by other community features such as productivity (but see Huston 1994) or number of trophic levels. The sheer complexity of possible interactions among species seems to have prevented us from achieving a clear knowledge of the factors that determine the presence, abundance, and dynamics of species in communities (Brown 1981, Simberloff 1982).

Experimental perturbation of natural communities is still the best way to study community dynamics. In particular, manipulating dominant predators or resource levels has helped us understand how these "top-down" and "bottom-up" forces filter through trophic levels (Powers

1992). For example, the removal of top predators in aquatic communities has been shown to produce "trophic cascades" in some systems, demonstrating the role of predation in limiting species (see, e.g., Carpenter et al. 1985, Kurmayer and Wanzenboeck 1996). The positive effects of nutrients on phytoplankton growth and subsequent effects on herbivores and higher trophic levels have also been documented (e.g., by Wallace et al. 1997). As the number of studies demonstrating interactions across trophic levels has increased, the focus of research has changed to determining the relative importance of top-down and bottom-up phenomena as a function of either characteristics of food webs or characteristics of the abiotic environment. For example, Proulx and Mazumder (1998) used a survey of published studies to suggest that plant species richness decreases with increased grazing in low-productivity environments but increases with grazing in high-productivity environments. Similarly, several studies in terrestrial systems have found that top-down effects of predators or grazers may be more prevalent when productivity is high: in essence that bottom-up effects must set the stage for top-down effects (Stiling and Rossi 1996, 1997, Fraser 1998, Fraser and Grime 1998, but see Belovsky and Joern 1995).

Such broad patterns among studies have great potential to increase our understanding of community dynam-

ics, but still, too few investigators conduct detailed manipulative experiments on communities. In particular, factorial experiments that manipulate both top-down and bottom-up forces are needed to determine how factors such as productivity affect the importance of predation and competition. Further, most previous studies quantify the response of species at a single point in time: such studies may not identify indirect effects such as trophic cascades. Only studies that follow community manipulations through time can separate short-term responses from long-term or equilibrium states.

We manipulated the presence of the top predator (the mosquito *Wyeomyia smithii*) and the basal trophic productivity (input of dead insects) in inquiline communities of the purple pitcher plant, *Sarracenia purpurea*, and followed the responses of the component species for 15 days. We used a pulse (rather than press) manipulation (Bender et al. 1984), in which the community is followed as it responds to a single perturbation. Our study was designed to determine whether populations in inquiline communities respond to perturbations of top predators "cascading" down trophic levels, perturbations of resource availability moving up from the lowest trophic levels, or by interactions between these two types of perturbations. If top-down effects control these communities, then removal of predators should cause cascading effects down through the invertebrate community. If bottom-up effects are more important in these communities, then the addition of dead insects should cause an increase in bacteria, with subsequent positive effects up through trophic levels. Interactions would be indicated if the effects of mosquito removals depended on the addition of dead insects or vice versa.

Materials and methods

The inquiline community

The purple pitcher plant, *Sarracenia purpurea*, has one of the most widespread distributions of all carnivorous plants, occurring from north Florida to Canada. Each plant may have from 1 to 12 cup-shaped leaves, each of which can hold up to 100 ml of water. The leaves collect rainfall and attract insects, which then drown in the water and are thought ultimately to serve as a source of nutrients for the plant.

The individual leaves also act as hosts for an active community of nonprey invertebrates (Fig. 1). Inquiline species include several dipterans that occupy pitchers during larval development, including the pitcher plant mosquito (*Wyeomyia smithii* (Coq.)) and midge (*Metriocnemus knabi* Coq.). These species, along with the pitcher plant mite (*Sarraceniopus gibsoni* (Nesbitt)) (Fashing and O'Conner 1984) and a bdelloid rotifer (*Habrotrocha rosa* Donner) (Bateman 1987, Petersen et al. 1997, Bledzki and Ellison 1998), appear to be found exclusively in *Sarracenia purpurea*. A number of other species are also commonly found in pitchers, including protozoans (Addicott 1974, Cochran-Stafira and von Ende 1998) and bacteria (Addicott 1974, Prankevicus and Cameron 1989, 1991, Cochran-Stafira and von Ende 1998). Although both invertebrates and plants may depend on the same potentially limiting resource, captured prey insects, inquilines confer a net benefit on plants by releasing excreted nutrients or by otherwise processing prey (Bledzki and Ellison 1998, Giberson and Hardwick 1999). There is a long history of studies on inquiline communities (e.g., Addicott 1974, Bradshaw and Creelman 1984, Miller et

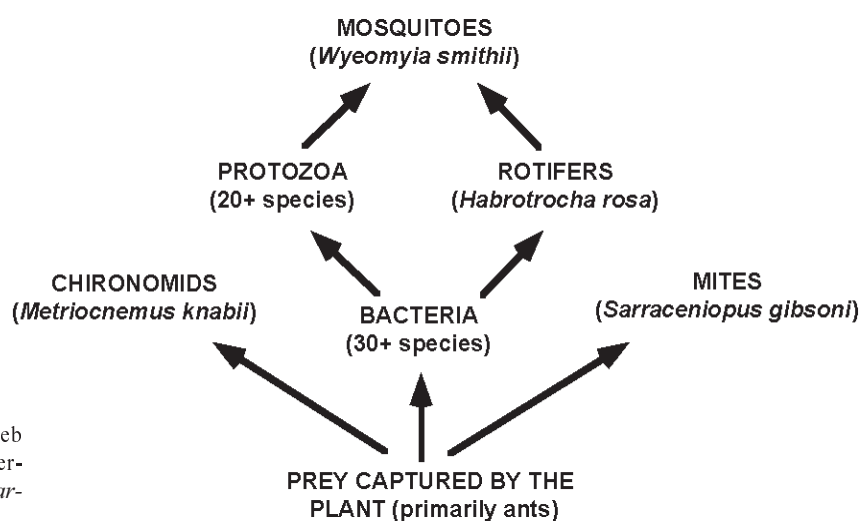


Figure 1. The hypothetical food web of phytotelmata found in the water-filled leaves of the pitcher plant *Sarracenia purpurea*.

al. 1994, Harvey and Miller 1996, Cochran-Stafira and von Ende 1998) and specific species therein (e.g., Istock et al. 1975, Bradshaw and Holzapfel 1986, 1989, Heard 1994).

Previous studies have documented interactions between mosquitoes, the top predator, and several other species in the community. Mosquito growth and development are directly related to food availability (Farkas and Brust 1985). Mosquitoes reduce protozoan (Addicott 1974) and bacterial (Cochran-Stafira and von Ende 1998) abundances and suppress growth of their own conspecifics (Miller et al. 1994). Further, Heard (1994) demonstrated a "processing chain commensalism" in that midges increased the food availability and growth rates of mosquitoes by feeding on dead insect prey, releasing nutrients and increasing bacteria growth.

Few studies have included analyses of bacteria, the lowest trophic level in *S. purpurea*. Dead insects are probably first consumed by bacteria: cell densities from the water in *S. purpurea* are frequently greater than 10^7 cells per milliliter. These bacteria are generally gram-negative rods (Cochran-Stafira and von Ende 1998, personal observation) and may include high abundances of anaerobic bacteria (Prankevicus and Cameron 1991), especially when prey are very abundant (personal observation). Addition of insect prey has been shown to increase the abundance of bacteria and protozoans (Kneitel and Miller 2002).

Field methods

We studied inquiline communities in a large, open savanna in the Apalachicola National Forest 6 km north of Sumatra, Florida (30° 05' N, 84° 59' W). This area is dominated by wiregrass (*Aristida stricta*) and *Sphagnum* spp. and harbors over 1000 *S. purpurea* along with several other carnivorous plants including *S. flava*, *S. psiticina*, *S. leucophyllum*, *Drosera rotundifolia*, *D. lineata*, and several *Pinguicula* and *Utricularia* spp. The *Sarracenia* species appear to be spatially segregated; *S. purpurea* occurs in the slightly higher, drier areas that make up the majority of the savanna.

Our experiment was designed to be a pulse perturbation (Bender et al. 1984). We directly manipulated both the presence of mosquitoes (top trophic level) and the input of dead insects (nutrient and carbon source) in a factorial design and then followed the responses of the species in the community at three-day intervals for 15 days. We first identified 20 plants with at least one water-filled pitcher in each of five different areas (blocks) of the savanna, and we designated one pitcher on each plant for

use in the experiment. Five of the 20 pitchers in each area were randomly assigned to each of four different treatments: all four combinations of mosquitoes removed or not removed and insects added or not added. We manipulated the abundance of mosquitoes by first removing all possible fluid (and the inquilines suspended in it) from all pitchers with first large and then small plastic pipettes. The pitchers were then rinsed out with sterile water. The mosquitoes from each pitcher were counted and were either removed (mosquito removal treatments) or replaced (no mosquito manipulation). The fluid was then returned to the pitcher of origin. Quantity of dead insect prey was manipulated by addition of a single autoclaved mealworm (mean = 0.105 g, standard deviation = 0.004) to each of half of the pitchers in each block; prey level in the remaining pitchers remained unmanipulated. We removed the contents of an additional two pitchers per block from the field to document the initial densities of inquiline species in the communities.

Treatments were initiated on 25 October 1996. Subsequently, a single pitcher from each treatment was harvested every three days from each of the five blocks. Each of the four combinations of community manipulations was thus replicated five times in a blocked design on each of five harvest dates (2 mosquito treatments x 2 dead insect treatments x 5 sample days x 5 blocks) for a total of 100 pitchers, each located on a separate plant.

Quantification of inquilines

The fluid from each pitcher was sampled for bacteria within 2 hours of harvesting. Serial dilutions with a saline buffer were used to create 10^{-4} , 10^{-6} , and 10^{-8} mixtures. A final 0.1 ml from each dilution was plated on a Luria broth agar plate and cultured at 24°C under a 12 hour light/12 hour dark cycle. Plate censuses at 48 and 72 hours were very similar: we present only the 48-hour results here. No attempt was made to identify bacterial strains: all analyses use colony types based on color, size, and texture.

A second sample of 1 ml was also removed for quantification of rotifers. Rotifers were counted on a Sedgewick-Rafter cell at 40x magnification. Although most rotifers observed were probably *Habrotrocha rosa*, we made no effort to differentiate species. All other inquilines in each sample were also counted. The remainder of the pitcher sample was preserved by addition of approximately 0.5 ml of saturated mercuric chloride and two drops of 0.04% bromophenol blue.

To quantify protozoa, we used a hemocytometer to observe two drops of the preserved sample. Pitcher plants are known to harbor a number of common protozoa, in-

cluding *Cryptomonas*, *Cyclidium*, *Bodo*, and *Colpidium* (Addicott 1974, Cochran-Stafira and von Ende 1998, Miller et al. 2002), but no attempt was made to identify protozoa to species in these samples. The preserved sample was censused at 10-40x for dipteran larvae, mites, cladocerans, and copepods. The sample was then photographed, and an image-analysis system was used to measure the body lengths of up to five randomly chosen mosquito larvae per sample.

Analysis

The abundance data for each individual species, along with bacterial richness and mosquito length data, were first analyzed by means of a full ANOVA including main

effects of harvest date, mosquito treatment, and prey-addition treatment, and all interaction terms. Abundance data were log transformed before analysis; species richness was first rarified by the methods of Gotelli and Entsminger (2001). In most cases, significant interactions occurred between harvest date and either or both the mosquito-removal or prey-addition treatments. Because the mosquito-removal and prey-addition treatments were of primary interest, separate ANOVAs were then calculated for each variable at each harvest date according to a simpler model of mosquito treatment, prey addition, and their interaction. Only these analyses are presented here.

Because of the large number of tests, details of each analysis (mean squares, sums of squares) are not provided

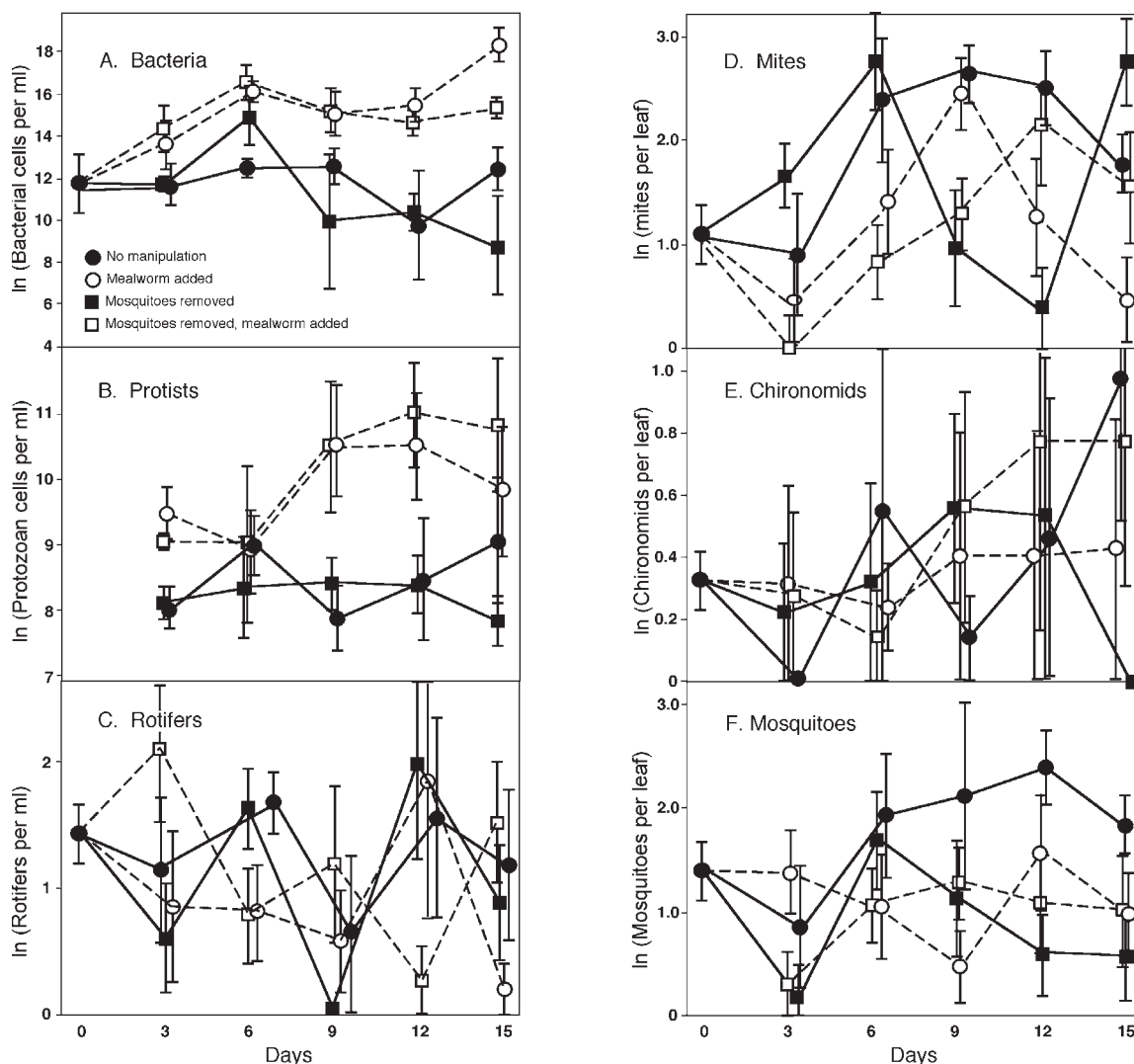


Figure 2. The effects of resource-addition and predator-removal treatments on major phytotelmata species over the 15-day experiment. Error bars represent standard errors around the means determined from five replicate communities. Open symbols and dashed lines show treatments in which mealworms were added; closed symbols and solid lines show treatments in which no mealworms were added. Squares represent treatments in which mosquitoes were removed; circles show treatments in which mosquitoes were not manipulated. Statistical tests of treatments on each day can be found in Table 1.

Table 1. F-values for effects of predator-removal (PR) and resource-addition (RA) treatments on various species in the pitcher-plant community. Values marked by asterisks are significant (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

		Day 3	Day 6	Day 9	Day 12	Day 15
Bacteria, cells/ml	PR	0.021	3.090	0.097	0.638	7.639*
	RA	5.254*	9.670**	5.937*	19.831***	37.414***
	PR × RA	0.290	1.377	0.183	0.029	0.182
Protozoa, cells/ml	PR	0.148	0.125	0.079	0.044	0.013
	RA	15.590***	0.148	10.729**	8.335*	4.761*
	PR × RA	0.657	0.235	0.158	0.213	1.502
Rotifers /ml	PR	0.370	0.022	0.008	0.550	0.875
	RA	1.282	6.402*	0.744	0.978	0.085
	PR × RA	2.119	0.009	0.889	1.915	2.208
Cladocerans /ml	PR	2.275	0.002	1.462	4.363	0.041
	RA	0.285	0.001	0.374	0.862	0.834
	PR × RA	1.320	0.338	0.374	0.005	0.708
Copepods /ml	PR	8.279**	0.107	0.001	0.455	0.001
	RA	1.024	1.280	0.697	0.009	2.950
	PR × RA	3.782	1.198	1.067	0.752	0.441
Mites /pitcher	PR	0.189	0.005	0.787	0.365	1.179
	RA	7.109*	1.348	0.001	0.039	1.326
	PR × RA	1.681	0.117	0.023	2.447	0.005
Chironomids /pitcher	PR	0.134	0.289	0.688	0.146	0.727
	RA	0.629	0.450	0.174	0.027	0.076
	PR × RA	0.306	0.015	0.194	0.078	2.345
Mosquitoes /pitcher	PR	6.248*	0.018	0.028	6.050*	1.611
	RA	0.381	0.227	1.251	0.111	0.172
	PR × RA	0.169	0.016	2.134	1.398	1.868
Mosquito length	PR	0.021	6.172*	2.367	1.197	0.109
	RA	1.610	1.465	0.126	0.174	0.017
	PR × RA	0.169	0.905	0.090	1.897	0.016
Bacterial species richness	PR	1.500	0.133	0.044	1.038	0.529
	RA	0.001	1.200	2.162	6.609*	0.525
	PR × RA	2.667	0.133	0.044	0.285	4.764*

here. In all but one case, five replicates of each of the four treatment combinations were performed, resulting in 1 degree of freedom for each treatment and for their interaction (sample size was lower in the fourth harvest in one treatment because one pitcher was damaged and therefore omitted from the analysis). Because multiple statistical tests are conducted at each date, we must also be concerned about appropriate probabilities of Type 1 error. We prefer to not use Bonferroni adjustments, but to instead interpret results cautiously and to put greater weight on patterns that appear at multiple sampling dates.

Results

The pitcher damaged during the experiment was not included in the analyses. The remaining 99 pitchers held water until their harvest. In most cases, the remains of the added mealworm larva were still present in resource-addition pitchers.

Although the unmanipulated pitchers maintained a relatively constant bacterial density during the experi-

ment, bacterial abundances increased by an order of magnitude within three days after prey addition (Fig. 2A). This effect remained significant on all five census dates (Table 1). At the last harvest, bacterial density was also significantly lower in mosquito-removal pitchers, but prey addition and mosquito removal showed no significant interactions during the experiment.

Most pitchers harbored from 2 to 6 different types of culturable bacteria. After rarefaction of the data, neither treatment was found to affect consistently the number of bacterial types (Table 1). A positive effect of prey addition on number of colony types was significant only at day 12; throughout the experiment, neither mosquito removal nor any interaction showed a significant effect.

After only three days, protozoan abundances were an order of magnitude greater in communities with added prey (Fig. 2B). This effect was significant on all census dates except day 6 (Table 1). No significant effect of mosquito removal or interaction between prey addition and mosquito removal was ever observed.

The abundance of rotifers was largely unaffected by either treatment (Fig. 2C) except for a significant decrease in abundance with resource addition on day 6 (Table 1). Similarly to relatively rare species, copepods and cladocerans were generally unaffected by predator removal or resource addition (Table 1).

At day 3, mites were significantly less abundant in prey-addition pitchers than in controls (Fig. 2D). Thereafter, no significant effects on mite abundance were observed, although mites were generally most abundant in pitchers to which prey had not been added.

Despite removal of all mosquitoes at the beginning of the experiment, some mosquitoes were found in removal pitchers at day 3, and mosquito abundances there were significantly lower than those in control pitchers only on days 3 and 12 (Fig. 2F, Table 1). No effect of or interaction with prey addition was observed at any census. Mosquitoes in the removal pitchers were significantly smaller than those in control pitchers on days 6 (Fig. 3). Chironomid abundances were generally low and variable in all treatments and were not significantly affected by any treatment (Fig. 2E, Table 1).

Discussion

In the absence of outside disturbance, populations within communities should be limited either by resources for growth or by predation from higher trophic levels. In inquiline communities, the effects of resources on lower trophic levels were readily apparent - both bacteria and protozoa increased 10-fold after the addition of resources - but the higher trophic levels in this community were not affected by resource addition. The removal of a top preda-

tor, mosquitoes, had little effect on the community, perhaps because of the rapid recovery of mosquito populations in the removal pitchers.

The significant increase in bacterial and protozoan abundances in response to addition of prey occurred within three days and persisted through the entire 15-day experiment. This result is consistent with a body of theory and work on the effects of productivity on communities (e.g., Lindeman 1942, Hairston et al. 1960). Surprisingly, however, this effect was expressed uniformly by all bacterial types: few significant effects were evident on the number of colony types (Table 1) or relative abundances of colony types (data not presented here). Although our use of colony types is likely to have undercounted the number of actual species present, this lack of species-specific responses differs from the results of Cochran-Stafira and von Ende (1998), who found species-specific responses of protozoa to mosquito removal in laboratory communities of pitcher plant inquilines.

Also surprising was that prey addition did not increase species abundances higher up in the trophic structure (Table 1, Fig. 2). Gut analyses and observation reveal that rotifers, copepods, cladocerans, and mosquitoes all feed on protozoa (personal observation) and are also likely to feed on bacteria, yet none of these species consistently increased in abundance in response to prey addition; neither did mosquito size. Rotifers, copepods, and cladocerans have a generation time on the order of days and would have been expected to show increases in numbers if they were limited by bacterial and protozoan availability. Mosquito abundances are determined by egg-laying of adults and subsequent survival of eggs and juvenile stages (Heard 1995). Mites, whose diet and role in the commu-

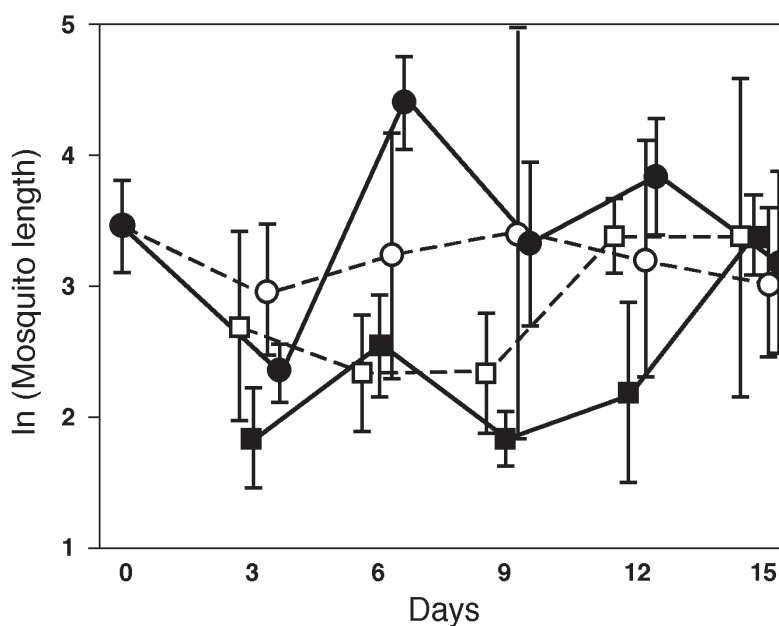


Figure 3. Effects of treatments on mosquito length over the 15-day experiment. Treatments are as in Figure 2. Bars represent standard errors around the means, determined from the mean mosquito length in five replicate communities. Statistical tests of treatments on each day can be found in Table 1.

nity are unknown, and chironomids, whose larvae feed in part on the dead insects that fall into the pitchers (Heard 1994), also showed no response to food addition.

Mosquito removal had virtually no effect on the abundance of any other species in the community, although studies in other systems have frequently found predator control of abundances in communities (e.g., Carpenter et al. 1985, Menge 1995, Schmitz et al. 2000). Our result is probably due to the "pulse" (Bender et al. 1984) nature of the design, which allowed the rapid recovery of the mosquitoes from the perturbation. By day 6, mosquito abundances were statistically indistinguishable from those in control pitchers. These newly hatched mosquitoes were smaller early in the experiment (Fig. 3) but were approximately the same size as those in control pitchers by the end of the experiment.

We do not know whether the recovery in mosquito numbers came from newly laid eggs or from eggs that remained in the pitchers after washing. Also, female mosquitoes may lay eggs preferentially in pitchers without mosquitoes (Bentley and Day 1989), although Heard (1994) found no effect of conspecific density on oviposition behavior in *Wyeomyia smithii*.

The lack of opportunity in our experiment for quantifying the effects of mosquito removal on the remaining community left little opportunity for interactions between the mosquito-removal and prey-addition treatments. Indeed, a pulse experimental design (Bender et al. 1984), which allows the recovery of manipulated abundances, may generally be a poor method for investigating interactions between top-down and bottom-up forces. A press experiment might yield more information on long-term interactions between mosquito removal and resource addition (Bender et al. 1984). Kneitel and Miller (2002) conducted such a press experiment in pitcher plants, holding mosquito and prey numbers constant at treatment levels. As in the present study, they found significant positive effects of prey addition on bacteria and protozoa, but in addition found positive effects on rotifers and mites. Further, their mosquito removal had the cascading effect of increasing rotifers and decreasing bacterial abundances. These differences from our results could reflect either differences in experimental design or seasonal differences in the importance of resources and predation.

Although the pulse design used here precludes quantifying effects of mosquitoes on the rest of the community, it does provide a measure of community resilience, the speed with which a community returns to some equilibrium following a perturbation (Pimm 1984). Clearly, this community is highly resilient to perturbations in mos-

quito abundances, as long as sources of new mosquitoes remain. The community would be much more affected by short-term perturbations of resource levels: in other words, resilience would depend on which part of the community were perturbed.

This work has concentrated on local, within-pitcher, phenomena as determinants of community patterns within pitchers, rather than potentially very important regional factors (Ricklefs and Schluter 1993). Inquiline communities in pitcher plants have been shown to vary in the numbers and abundances of component species at several different scales (Harvey and Miller 1996). The causes of this variability are unclear but may be related to stochastic immigration of key species or capture of prey (resource input; Cresswell 1993), abiotic conditions around the pitcher, physical characteristics of the pitcher itself (Wolfe 1981, Cresswell, 1991), or age of the community (Fish and Hall 1978). Our study shows that prey addition could contribute significantly to among-community variation through dramatic increases in bacterial and protozoan abundances, but the effects of prey addition were not apparent at higher trophic levels. It is difficult to determine from our results whether variation in either the migration or the establishment of the mosquito *Wyeomyia smithii* contributes to the overall variation in inquiline communities. Experiments that incorporate migration and other regional factors, along with the local factors demonstrated here, will be necessary to elucidate the relative importance of each in structuring communities.

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