Top-down and bottom-up forces within the northern pitcher plant (*Sarracenia purpurea*) inquiline food web: a study using the pitcher plant midge (*Metriocnemus knabi*)

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Abstract

The objective of this study was to examine the effects of top-down (predation) and bottom-up (resource) forces within the inquiline community of the northern pitcher plant, *Sarracenia purpurea*. The northern pitcher plant is a carnivorous plant that relies on organisms living inside its leaves to decompose its prey. These organisms compose a complex food web with the pitcher plant midge larva, *Metriocnemus knabi*, being the primary producer and the pitcher plant mosquito larva, *Wyeomyia smithii*, being the top predator. Previous studies suggest that the inquiline food web directly benefits from increased *M. knabi* production. Experimental manipulation of top-down forces within this isolated food web shows that predation plays a significant role in decreasing populations at lower levels of the food web. Resource manipulations did not indicate that the inquiline community is resource-limited. Midge processing had a significant effect on bacteria densities, but did not influence densities at higher trophic levels. These results suggest that top-down forces have a significant effect on the inquiline food web, but bottom-up forces have variable effects.

Introduction

The northern pitcher plant, *Sarracenia purpurea*, is a carnivorous plant that is widely distributed throughout eastern and central North America (Heard 1994). These plants grow in nutrient-poor bogs and fens. Pitcher plants compensate for the lack of nutrients in the soil by absorbing decomposing arthropod carcasses that get trapped in their vase-shaped leaves. The pitcher plant's modified leaves catch rainwater and invertebrates fall into the rainwater and drown (Ellison et al. 2003).

Inquilines living within the phytotelm (small body of water) of the pitcher plant aid in decomposition of the invertebrate carcasses (Bradshaw 1983). These inquilines include the pitcher plant mosquito larva, *Wyeomyia smithii*, the pitcher plant midge larva, *Metriocnemus knabi*, the pitcher plant flesh fly larva, *Blaesoxipha fletcheri*, bacteria, protozoa, rotifers and water mites. The midge, flesh fly and mites feed on the invertebrate carcasses and release physically or chemically processed particles into the water (Bradshaw 1983). Bacteria then feed on these small particles. Rotifers and protozoa feed on bacteria. The pitcher plant mosquito is the top predator and preys on rotifers, protozoa and bacteria (Cochran-Stafira and von Ende 1998).

Food webs are affected by bottom-up (resource) and top-down (consumer) influences. Bottom-up factors involve the decomposition of resources by the processing detritivores which provide nourishment for the rest of the food web. Changes at the bottom of the food web can have an effect on the entire food web. Studies have shown that increased resource decomposition will result in an increase in biomass at higher trophic levels in the pitcher plant inquiline food web (Ellison et al. 2003). Top-down regulation occurs when higher trophic levels control the populations of lower trophic levels through predation. Changes in predator density can affect the rest of the food web. For example, Addicott (1974) found that species diversity within the inquiline food web declined when mosquito density increased.

The inquiline food web within the northern pitcher plant is experimentally advantageous for studying food web dynamics because it is an isolated community that is easily manipulated. Also, pitchers found in the field can be used for natural experimentation.

Experiment and Hypotheses

A broad survey of pitcher plants was conducted at bogs located on the UNDERC property. I surveyed data for mosquito and midge densities, fluid coloration, and lip diameter. I looked for a simple correlation between the mosquito and midge densities.

The experiment involved manipulation of predator, midge, and prey densities. The purpose of this experiment was to determine the role of the pitcher plant midge in the inquiline community and examine its affects on top-down and bottom-up forces.

Given past research, I hypothesized that my survey would yield a correlation between midge and mosquito densities. Heard (1994) found that the mosquito density within the inquiline food web depends on the midge density. High midge density will increase resource decomposition, which will increase bacterial density. As a result, mosquitoes will prosper from the abundant food source and their density will increase.

Secondly, I predicted that mite density would not increase nor decrease in response to mosquito density (Heard 1994), while protozoan and rotifer densities would decline in response to increased mosquito density (Addicott 1974).

Because mites are also processing detritivores, their relationship to the mosquito will be similar to that of the midge and mosquito. However, mosquitoes feed on protozoa and rotifers. Therefore, according to food web theory, increasing predator density would decrease prey density.

Thirdly, I hypothesized that mite, protozoan, rotifer and bacteria densities would increase with increased resource availability (Ellison et al. 2003). Addition of prey to the pitchers would result in increased density of the mites that feed on them. Bacteria density benefits from resource addition because of increased midge processing rates. As a result, the protozoa and rotifers which feed on the bacteria would increase in number.

Finally, I predicted that increased midge density would result in increased mite, protozoa, rotifer, and bacteria densities. Increasing midge density would increase resource processing rates. Therefore, bacteria density would increase as the result of increased midge activity. The organisms that feed on the detritus and bacteria would thus respond to increased detritus and bacteria densities.

Materials and Methods

The experiment was conducted at the University of Notre Dame Environmental Research Center (UNDERC) in the Upper Peninsula of Michigan between May 16, 2005 and July 22, 2005.

A survey of pitcher plant leaves was conducted at Tuesday Bog and Tender Bog. The fluid within each pitcher was pipetted out and deposited in a dish. Mosquito and midge abundance, water clarity and lip diameter were measured. The mosquito and midge densities were counted with the naked eye. The fluid was returned to the pitcher plant after the dipterans are counted. The collected data was analyzed for correlations between the midge and mosquito densities.

The experiment included three fully-crossed factors: top-predator density, resource abundance, and midge abundance. I measured mite and rotifer densities, and protozoa biovolume and species richness.

I collected fluid from 60 pitchers and used the dipterans for the food web manipulations. The pitchers were cleaned of as much debris as possible. However, the base of each pitcher was plugged with wax to avoid the mixing of any left-over debris with my experiment. I then replaced the fluid with fixed numbers of midges, mosquitoes and prey carcasses for the experiment.

Top-down manipulation occurred at two levels with the addition of zero or 15 mosquito larvae. Resource abundance was manipulated at three levels: addition of zero, four, and 20 mg of ants in the same 60 pitchers. Finally, midge density will be manipulated at two levels with pitchers containing zero and 16 midges.

The fully-crossed design had a total of 12 combinations, replicated five times. The pitchers were covered with netting to prevent insects from falling into the pitchers or mosquitoes from ovipositing in them. Sampling occurred once a week for four consecutive weeks. Sampling entailed extracting the liquid from the pitchers to analyze and maintain treatment densities. Mosquito and midge counts were done with the naked-eye at the bogs. A 100μL water sample from each pitcher was taken to the lab where mites, protozoa, and rotifers were counted using a microscope. The data collected was analyzed using repeated measure, multi-way ANOVA and post-*hoc* Tukey tests on SYSTAT software. Rotifer densities were log-transformed for statistical accuracy.

Results

I surveyed 66 pitchers in Tuesday Bog and Tender Bog. I did not find a correlation between midge and mosquito densities ($r=0.263$, $p=0.033$). The significant p-value is not an accurate evaluation of the data because a large percentage of the sampled pitchers contained low midge and mosquito densities. The r-value is a better indication of the actual correlation.

All experimental results are based on the data collected from sample sessions one through three because 32 of the pitchers were destroyed by an animal before the fourth sampling session. Also, due to low mite density in the samples, I was unable to accurately evaluate the effects of top-down and bottom-up forces on these organisms.

Average protozoa biovolume (μm^3) was used as a quantitative measure of protozoa abundance in a single Palmer cell. Increased mosquito density had a negative effect on average protozoa biovolume ($p=0.004$, $df=1$;Figure 1). However, there was a significant interaction between mosquitoes and midges ($p=0.044$, $df=1$;Figure 1). Increased resource availability did not have a significant effect on protozoa biovolume ($p=0.450$, $df=2$). Increasing the number of midges in a pitcher was found to have a marginal negative effect on average protozoa biovolume ($p=0.054$, $df=1$;Figure 1).

Both midges ($p=0.021$, $df=1$) and mosquitoes ($p<0.001$, $df=1$) had a significant negative effect on rotifer density (Figure 2), but their interaction was not significant ($p=.284$, $df=1$). Ant treatments did not significantly influence rotifer density ($p=0.753$, $df=2$).

Bacteria density was only tabulated from sample session two because we were unable to gather sufficient samples from the destroyed pitchers from sample session four. Increased mosquito density had a negative effect on bacteria density within the pitcher plants ($p=0.028$, $df=1$;Figure 3). Increased midge density had a positive effect on bacteria density ($p=0.031$, $df=1$;Figure 3). Resource availability did not have a significant influence on bacteria density ($p=0.375$, $df=2$).

Discussion

My experiment suggests that top-down forces have a significant effect on inquiline communities. However, the influences of bottom-up forces were variable. Resource manipulations did not have a significant effect on the food web, and midge processing only yielded a positive response from bacteria density.

Heard (1994) suggested that *W. smithii* density is dependent on *M. knabi* processing of arthropod carcasses that fall into a pitcher. I did not observe a correlation between mosquito and midge densities in my survey of 66 pitchers in the field. Therefore, I question the relative importance of the midge-mosquito relationship within the northern pitcher plant.

Kneitel and Miller (2002) found that increasing top predator density in the inquiline food web of the northern pitcher plant, *S. purpurea*, decreased rotifer density, but did not affect protozoa abundance. They proposed that protozoa were more resistant to predation than rotifers. The same study observed that bacteria abundance increased with increasing predator density. Kneitel and Miller suggested a trophic cascade model in explanation for this result.

Increased mosquito density had a negative effect on rotifer density, average protozoa biovolume, and bacteria density. Given my results, I question whether or not a trophic cascade model is appropriate for this system. Instead, my results support Addicotts (1974) finding that high predator density has a strong negative effect on total number of prey individuals.

Kneitel and Miller (2002) concluded that increasing resource availability promoted bottom-up effects throughout the inquiline food web of the northern pitcher plant. In their experiment, Kneitel and Miller (2002) found that mites, protozoa, rotifers, and bacteria abundances increased in response to prey addition, suggesting that these organisms are resource limited. In contrast, my experimental results show that resource availability did not have a significant effect on average protozoa biovolume, rotifer density, or bacteria density.

The findings of my bottom-up experiment oppose accepted food web theory. I suspect that our methods of plugging the pitchers may have been inefficient. The leaf of the pitcher plant is trumpet-shaped, and midges prefer to burrow deep into the pitcher where arthropod carcasses and detritus accumulate. I plugged the pitchers with wax to prevent built up detritus from entering the resource pool of the food web and the midges from burrowing in it. This method has never been attempted in previous pitcher plant food web studies because either midges were not the object of study, or the experiment was performed in the laboratory. I suspect that the wax did not completely plug the pitcher or prevent the midges from processing the detritus. Therefore, all of the experimental pitchers had approximately equivalent resource availability, making my imposed treatments ineffectual.

The loss or gain of midges in the pitchers might also have been the result of the wax not sealing off the detritus. However, I replaced or removed midges at each sample session to maintain the experimental manipulations. My results show that midges had a negative effect on rotifer density. In theory, midge productivity should promote rotifer abundance because rotifers feed on bacteria. A possible explanation for my observation is that midges passively prey on rotifers. I noted that rotifers tend to be found feeding on large pieces of debris under the microscope. It is possible that midges accidentally consume these rotifers while feeding on arthropod carcasses. This is not out of the question considering that midges have jaws large enough to consume a rotifer.

I found midges to have a marginally negative effect on protozoa, which is also contrary to previous studies. However, my results show a strong midge-mosquito interaction. This interaction results from a significant negative effect of mosquitoes on protozoa. Therefore, the negative influence of midges on protozoa can be attributed to the midge-mosquito interaction, rather than midge influence alone.

Heard (1994) suggested that increasing midge density will increase resource processing rates, which provides increased resource availability for higher levels of the food web. This theory suggests that the midge is an essential component of the inquiline community structure within the northern pitcher plant. My results are inconclusive as to the relative importance of the midge within this food web. Bacteria density responded to increased midge production, but protozoa and rotifer densities did not. Further studies will have to be conducted to accurately determine the relative importance of the pitcher plant midge on top-down and bottom-up forces within this inquiline food web.

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Figures

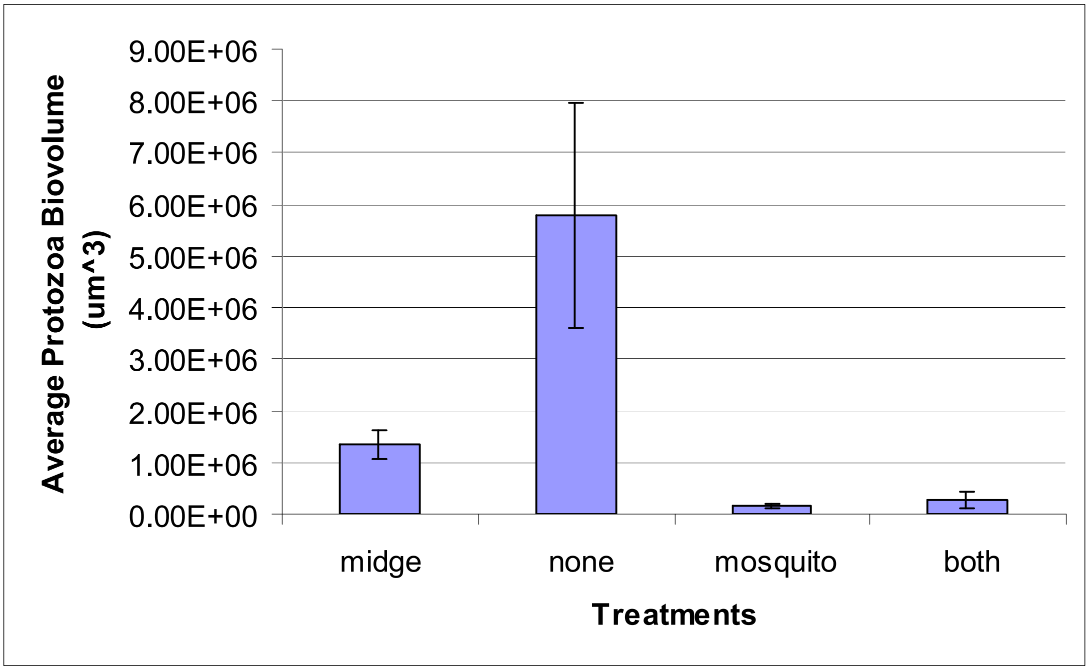

Figure 1. Treatment effects on average protozoa biovolume.

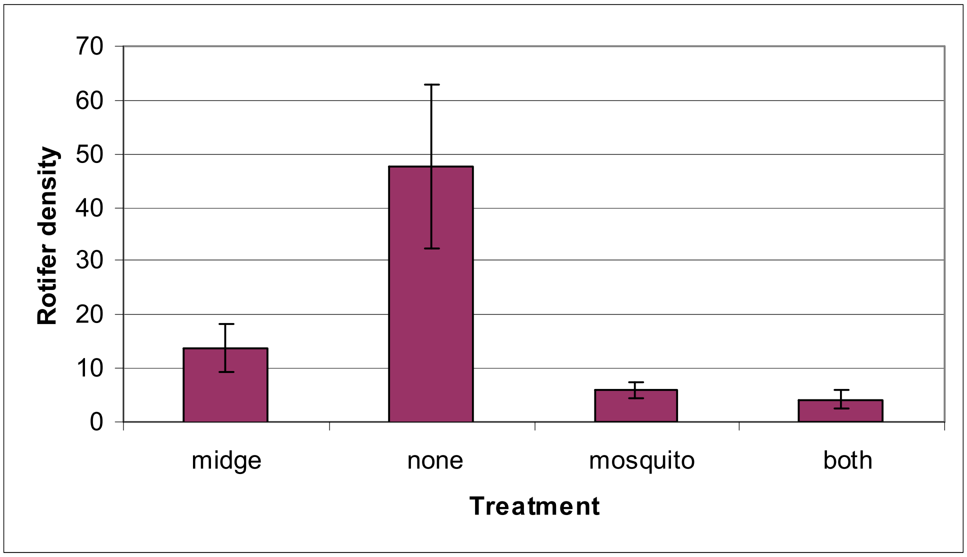

Figure 2. Treatment effects on rotifer density.

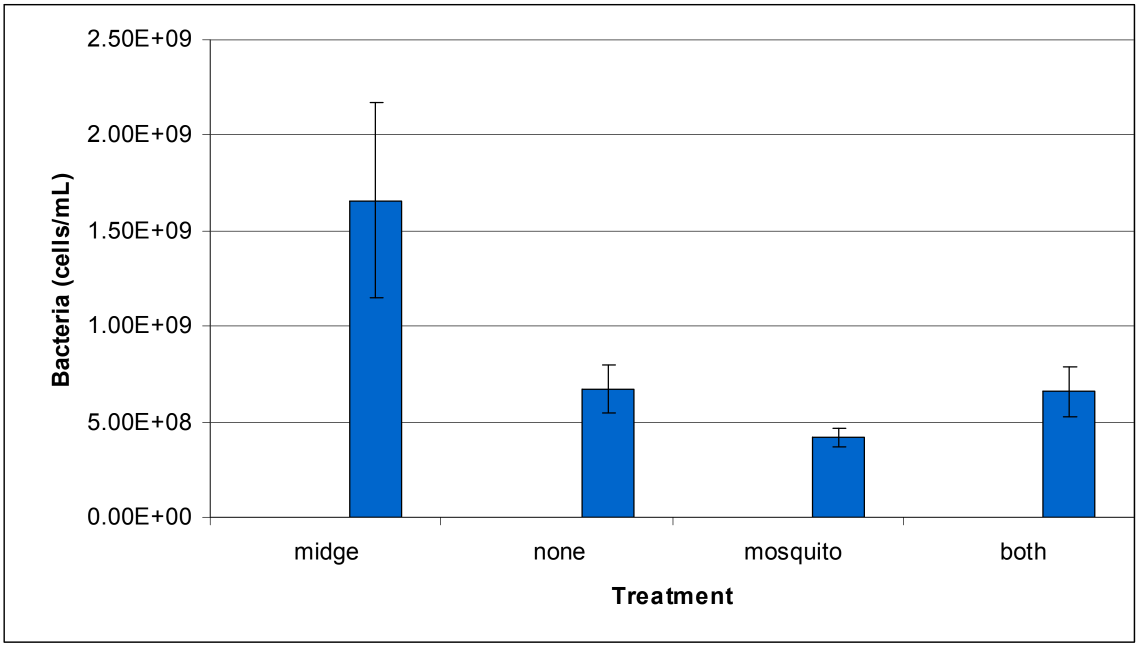

Figure 3. Treatment effects on bacteria density.