Inquiline Species Distribution among *Sarracenia purpurea*

UNDERC

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**Abstract**

Many studies have been done on the inquiline community existing within the carnivorous plant *Sarracenia purpurea.* Organisms within the community compose a model food web and break down insects trapped by the plant. This process releases nitrogen, carbon dioxide, and other nutrients which are absorbed by the plant. The intent of this study was survey inquiline communities at various spatial scales, and based on this survey, to identify any random, regular, or gradient of species distribution over a delineated area. Species richness was predicted to be the same among pitcher plant communities in a given bog. A nested sampling survey of Cranberry Bog on the UNDERC property was conducted to test this prediction. ANOVA and Tukey tests showed that protozoa abundance was not significantly different between the five sites. However, significant differences in protozoa species richness did exist between the five sites ($p<0.05$). Local comparison found that plants within a site did not significantly differ in species richness ($p>0.05$). Similar protozoa abundance is expected if protozoa are dispersed in the same manner. Differences in inquiline diversity between pitchers can possibly be attributed to differential predation, competition, or resource abundance. Further testing is needed to explain the spatial distribution of the inquiline species identified.

**Introduction**

The carnivorous plant *Sarracenia purpurea* is distributed throughout
North America from Florida to northern Canada.  It is found mainly in low
nutrient sphagnum bogs where it has a competitive advantage for light and
resources.  The pitcher of the plant is formed by its leaf, which is annually
regenerated in early spring.  From then on, one new leaf is produced every twenty
days (Giberson and Hardwick, 1999).  Closed until mid-summer, the leaves
collect rainwater upon opening, and this water is retained through the year.
Insects are attracted to the leaves, and fall into the water within.   Downward-
pointing hairs on the leaves of the pitcher prevent escape, and the insects
eventually drown.  The wall of the pitcher absorbs the nutrients derived from the
drowned arthropods, gaining nitrogen, carbon dioxide, and other nutrients which
are scarce and for which the plants compete in low nutrient bogs (Breeman, 1995;
Chapin and Pastor, 1995).

Pitcher plants were initially of interest to scientists because of their
carnivorous diet.  They are also recognized for housing a small aqueous
community within their pitchers.  These aquatic mesocosms are home to several
different inquilines, organisms whose habitat is contained within another.  These
organisms interact in a mutualistic relationship with the plant by producing
ammonia and carbon dioxide, which are absorbed by the plant and exchanged for
oxygen (Bradshaw and Creelman, 1984).  The dynamics of the inquiline

community can be represented by a simple food web (Figure 1).  Multiple

characteristics of the plant and its inquilines make the system ideal for study.  The

ephemeral nature of the pitchers forces the inquilines to disperse to nearby

pitchers before the leaves die, ensuring that extinction of inquiline species will

rarely occur because of the short lifetime of their habitat.  Replication of testing is

made possible by the high abundance of pitchers in one area.  Finally,  the short

generation time of the inquilines allows experimentation using several generations

of  aquatic invertebrates in a small time frame (Ellison et al., 2003).

The inquiline food web (Figure 1) is composed of three main trophic

levels.  The top level consists of the pitcher plant mosquito *Wyeomyia smithii*, the

second level of protozoa and rotifers, and the basal level of bacteria.  Together

with the plant, this community aids the plant with the digestion of drowned

arthropods found within the pitcher.

Digestion begins with the comminution of a drowned arthropod carcass by

the three processing detritivores.  These three species are the pitcher plant flesh

fly *Fletcherimyia fletcheri*, the pitcher plant midge *Metriocnemus knabi*, and

slime mite *Sarraceniopus gibsonii*. All three species feed upon the drowned

arthropod carcasses.

Coexistence of the predacious pitcher plant mosquito and the processing

detritivores is made possible by spatial partitioning of the aquatic environment

(Bradshaw and Creelman, 1984; Giberson and Hardwick, 1999).  The pitcher

plant mosquito filter-feeds throughout the water column and consumes the arthropod detritus and smaller organisms, the pitcher plant midge remains at the bottom of the pitcher, and the pitcher plant flesh fly stations itself at the surface to feed upon the prey as it enters the water.

After the carcass is processed into fine particulate matter, bacteria consume the detritus. Bacteria are the major food source for protozoa and rotifers. The omnivorous mosquito consumes all of these organisms, as well as detritus. This consumption of bacteria releases nutrients to the plant that would otherwise remain stored within the bacteria (Giberson and Hardwick, 1999).

Differing densities of predators and resources can have major effects on the community composition. By manipulating the densities of predators and arthropod carcasses in the pitcher environment, Cochran-Stafira and von Ende were able to investigate the effects of interspecies competition (1998). They found that higher densities of the pitcher plant mosquito allowed for greater species diversity in the protozoa population, as well as a greater concentration of bacteria. Without the presence of the mosquito, the bacteria population diminished, and there were fewer species of protozoa present, displaying the importance of the omnivorous predator as a keystone species, promoting diversity in the community (Ellison et al., 2003). However, a study of predator density conducted by Addicott concluded otherwise. Instead of increasing numbers of protozoan species, he found that omnivorous mosquitoes lowered numbers of all

species of protozoa present, and had no effect on species richness. Consequently, the mosquito was not categorized as a keystone species (Addicott, 1974). If the latter finding is a more accurate representation of inquiline interactions, predation will decrease species richness.

Along with interspecific competition and predation, other important factors influencing species diversity in this system have been studied. Kneitel and Miller studied three possible influences of species diversity: the densities of predators and resources, and dispersal frequencies. Of these three factors, only higher dispersal resulted in increased diversity. When dispersal frequencies were increased in the absence of predators, community diversity increased. At the same time, differences in inquiline composition between regional communities decreased (Kneitel and Miller, 2003).

Though the dipteran species disperse by oviposition, the protozoa and rotifers do not (Giberson and Hardwick, 1999). The primary method for rotifer and protozoa dispersal is passive dispersal via wind and rain, as opposed to phoresy, the dispersal of smaller organisms by traveling on larger vertebrate carriers (Caceres and Soluk, 1999).

The intent of this study was to survey inquiline communities at various spatial scales, and to identify any random, regular, or gradient of species distribution over a delineated area. Because several inquiline species disperse using similar mechanisms, such as rain and oviposition, inquiline composition in

different pitchers could be the same. Regardless of the spatial distribution of the pitchers on a local scale, species richness could depend on the spatial range of dispersal mechanisms.

Based on the literature reviewed above, species richness was predicted to be the same among pitcher plant communities in a given bog. Because the key predator of the inquiline community is dispersed by oviposition, it could be present in similar quantities throughout the bog. The protozoa and other bacterivores on which the mosquito feeds, disperse by passive mechanisms. However, if inquiline communities are found to differ in their species richness, these differences could be attributed to differential predation, competition, or resource abundance.

**Materials and Methods**

This study was conducted at Cranberry Bog at UNDERC in Gogebic County, Michigan Upper Peninsula.

A survey of pitcher plant communities was conducted using a nested sampling design. To conduct this sampling, five equidistant areas were identified and flagged in Cranberry bog (Figure 2). Within these five sections, three equidistant subsections were located, and three plants within each subsection were chosen for the study. In total, forty-five pitcher communities were surveyed.

Surveying the contents of the community was conducted in two different weeks. In the first week, I counted the numbers of larval dipterans. The contents

of the pitcher were removed using a plastic pipette, and transferred to a petri dish.

In the dish, flesh flies, midges, and mosquitoes were counted with the naked eye.

The second week of sampling, I collected samples of pitcher water, again

with the use of plastic pipettes, and stored them in microcentrifuge tubes.  Using

Palmer cells and a microscope, the protozoa, mites, and rotifers present in the

water were counted.  One Palmer cell of 100μl was read for each pitcher.

Pitchers used in the survey were those found growing in the same general

condition.  If possible, pitchers in shade, abnormally larger or smaller than the

average size, those too near the edge of the bog, or in other variant situations were

not chosen for the study.

Data analysis was conducted using SYSTAT 8.0 to examine any

relationships in species presence, absence, or quantity.  ANOVA was used to

calculate any possible relationship in  community composition between the

different pitchers at various scales.

**Results**

The first week's survey of midges, mosquitoes, and flesh flies did not

expose any significant differences in organism abundance throughout the bog

($p > 0.05$).

Protozoa abundance (Figure 3) does not differ significantly throughout

Cranberry Bog ($p = 1.441$).  Pairwise comparison using Tukey testing identifies

sites 2 and 4 as being most different (p=0.200), though the difference is not statistically significant.

There is a statistically significant difference of protozoa species richness between sites within the bog (p<0.05) (Figure 4).  Further analysis by pairwise comparison shows that site 2 is statistically different from all sites other than site 5, which is significantly different from sites 1 and 4.

Direct comparison of pitchers on the local scale (i.e., sub-samples within one site) yields no evidence of a significant difference in total abundance of protozoa.  Local comparison of species richness also yields no significant differences (p>0.05).

**Discussion**

Numbers of protozoa existing in *Sarracenia purpurea* are found to be the same by large-scale comparison (p=1.441).  This does not completely confirm protozoa dispersal by wind and rain supported by Caceres and Soluk (1999) because it does not identify dispersal patterns by species, but by organism type as a whole, and does not identify any mode of dispersal.

If wind and rain were the main factors influencing dispersal, species richness is expected to be statistically similar across a large area.  In the bog studied, species richness within pitchers differs significantly throughout the bog (p<0.05).  Means of dispersal is indeterminate from these results, but there are also no significant differences found from comparison of local communities.  This

leaves a possibility either of patterned protozoan dispersal, or of species specific modes of dispersal.

Although testing was as controlled as possible, several anomalies may have had influence on results. One such anomaly involves site 5. Pitchers at this site originally held water during the first week of experimentation, but the water was no longer present in the second week of the survey. This may have had significant effects on data for protozoa richness and numbers on both local and large-scale analyses. Other discrepancies are likely to have resulted from improper protozoa categorization. Because protozoa were categorized by physical characteristics and not to species, errors in identification could likely have resulted.

As was found by Kneitel and Miller, dispersal rates of inquilines can influence community richness and decrease regional variability between pitcher communities (2003). Several inquiline species disperse using the same method, making it possible for all communities within a region to have similar species composition. If species were found to have gradient or patterned dispersal, this would support inquiline dispersal as the major influence of community composition. If results showed differing community composition, further studies could include assessments of resource and predator abundance. In general, testing the northern pitcher plant system in this manner will help elucidate community dynamics within the pitcher and with the surrounding environment.

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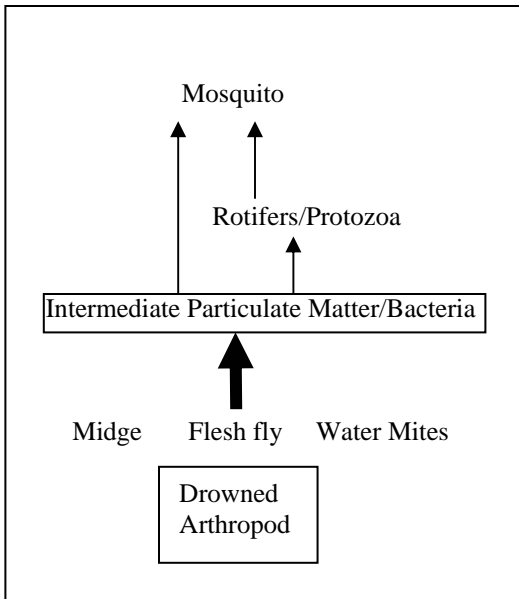
**Figures**



*Figure 1. The simple food web contained within the aquatic environment of the northern pitcher plant. Decomposition of drowned arthropods is begun by the pitcher plant midge, flesh fly, and water mite, resulting in particulate matter. The bacteria feed upon the intermediate detritus, and are in turn eaten by the rotifers and protozoa. Being a top-level predator, the mosquito also consumes bacteria, but feeds upon the rotifers and protozoa, as well.*
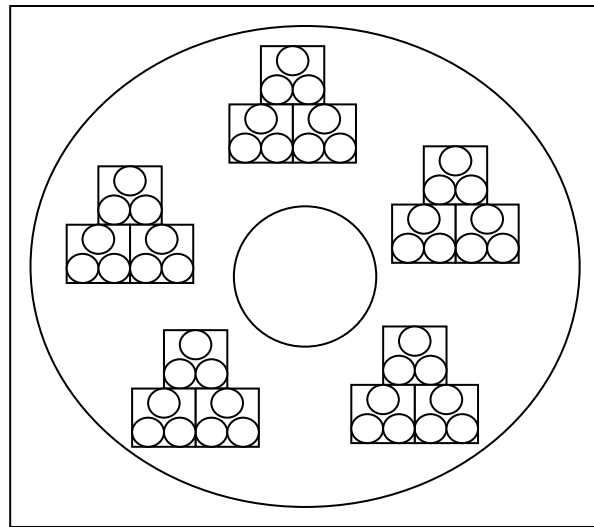


*Figure 2. An overhead depiction of the nested sampling design used during a survey of forty-five northern pitcher plants in Cranberry Bog.*
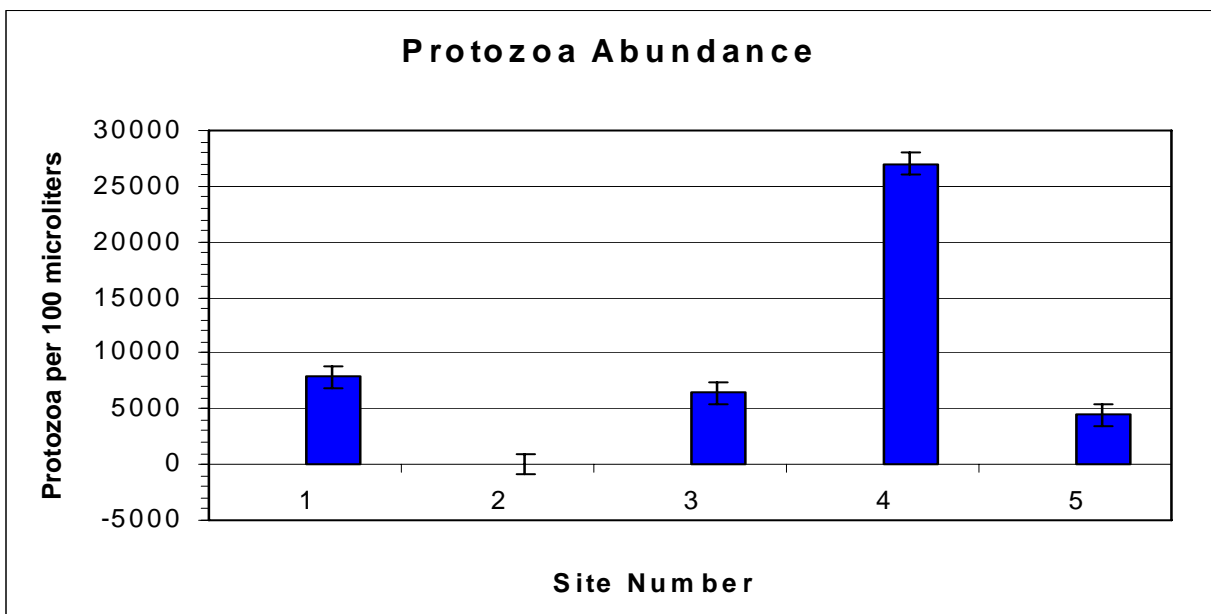


*Figure 3. Visual representation of results from ANOVA and Tukey comparison tests analyzing protozoa abundance of all five sites. By this comparison, none of the sites are found to be statistically different from the others.*
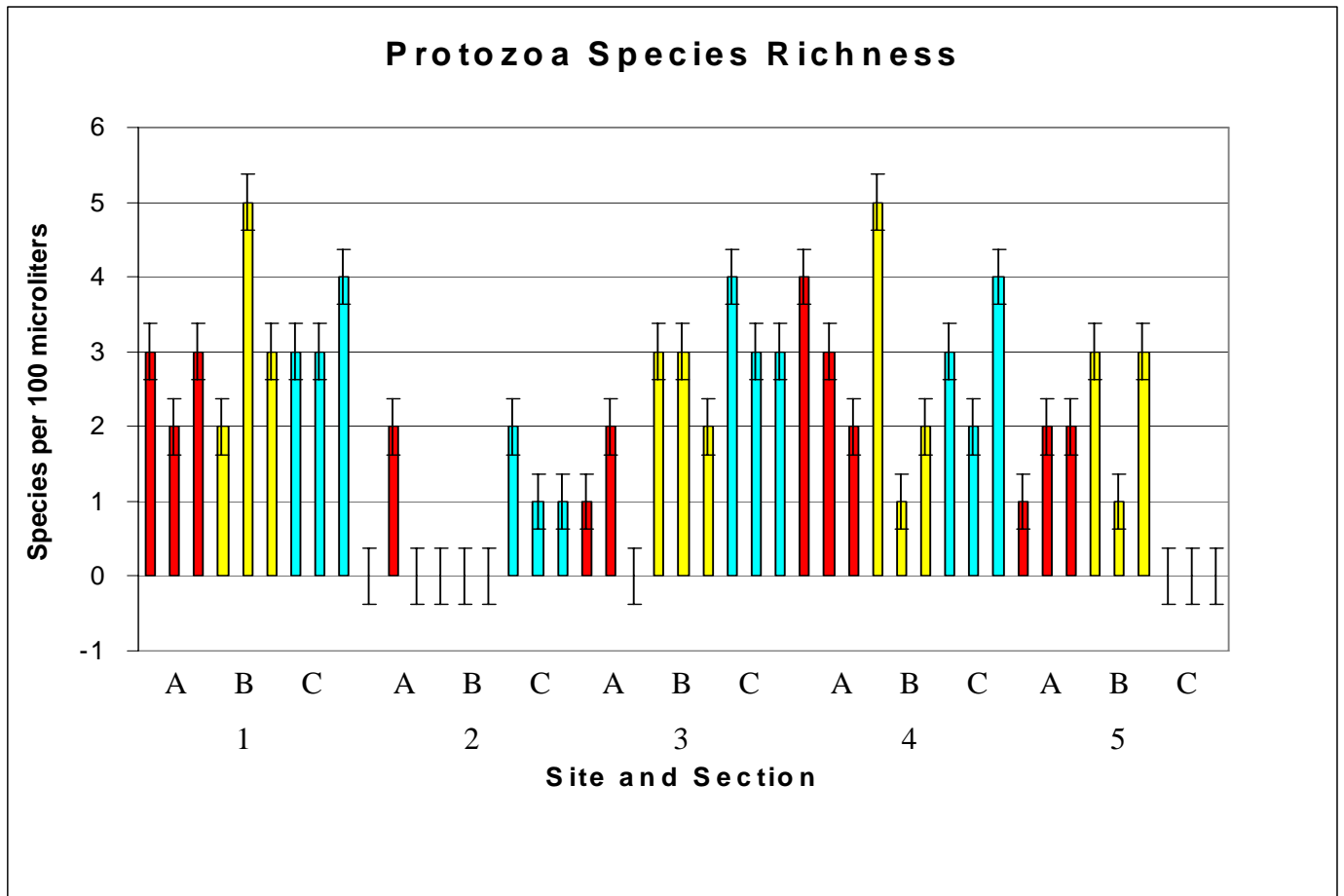
**Figures**



*Figure 4. Results of an ANOVA and Tukey tests comparing species richness among all five sites. There are significant differences between site 2 and sites 1,3, and 4, as well as between site 5 and sites 1 and 4.*

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