

**Inquiline diversity of the purple pitcher plant (*Sarracenia purpurea*) as a function of
pitcher isolation: the role of dispersal in metacommunities**

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“To understand the relative impact of any ecological process in structuring communities, it is essential to understand the spatial and temporal scale relevant for the particular question being addressed” (Addicott et al. 1987 as cited by Cáceres and Soluk 2002).

Abstract: Increasing empirical evidence suggests that patterns of diversity depend on the spatial scale being observed. For example, local communities linked by dispersal (“metacommunities”) are not only affected by those processes that operate *within* the community (such as predation and competition), but also by those that operate on a larger scale (such as migration *between* communities). The purple pitcher plant *Sarracenia purpurea* provides an ideal opportunity to explore the dynamics of metacommunities because of the discrete nature of the phytotelmata inhabited by a unique suite of easily manipulated aquatic organisms. Using methods inspired by Simberloff and Wilson’s study on the recolonization of seven islands in Florida Bay (1969-1970), this study sought to determine the extent to which pitcher plant isolation affects the diversity of the inquiline community that can colonize it. It became clear, however, that such a study is premature; the dispersal mechanisms, rates, and range of distances of which inquilines are capable must be determined first.

INTRODUCTION

A primary goal of community ecology is to determine the patterns that shape the distribution, abundance, and interaction of species. Traditionally, community theory has focused on the processes that govern diversity on a local scale, assuming local habitats to be closed or isolated (Leibold *et al.* 2004). A growing number of studies suggest, however, that patterns of diversity vary with the scale of observation; this, in turn, suggests that different processes may operate at different spatial scales (Leibold *et al.* 2004; Cadotte and Tadashi 2005). For example, previous studies have demonstrated that interspecific interactions (such as competition and predation) affect diversity on a local level, while the dispersal of individuals between local communities affects diversity on a regional level (Kneitel and Miller 2003; Leibold *et al.* 2004; Cadotte and Tadashi 2005). Such communities linked by dispersal are termed “metacommunities” (Hanski and Gilpin 1991; Wilson 1992 as cited by Kneitel and Miller 2005).

The impact that dispersal can have on community structure varies; studies have demonstrated that it can both increase and decrease local diversity depending upon dispersal rate and intensity (Leibold *et al.* 2004; Cadotte and Tadashi 2005). For example, rescue effects, the

prevention of local extinction of species by immigration (Brown and Kodric-Brown 1977 as cited by Miller and Kneitel 2005), and mass effects, the net flow of individuals created by differences in population size or density (Shmida and Wilson 1985 as cited by Miller and Kneitel 2005), can increase diversity. Furthermore, the degree of habitat or community *isolation* also matters. Habitats closer to a source population are more likely to receive dispersers from that population; this, in turn, increases the likelihood that a species new to the habitat will immigrate (a posit of island biogeography theory; MacArthur and Wilson 1963; Maguire 1963; Lack 1970; Rickfels 1977 as cited by Moody 2000). On the other hand, dispersal can also decrease diversity by reducing the effects of spatial refuges, or by encouraging homogenization of local community structure (Cadotte and Tadashi 2005). In short, the role of dispersal in shaping the diversity observed at multiple spatial scales remains unclear; additional empirical study is necessary.

The inquiline communities that inhabit the leaves of the purple pitcher plant (*Sarracenia purpurea*) provide an excellent system in which to study the role and range of dispersal of members of a metacommunity (Kneitel and Miller 2003). The discrete nature of individual leaves, plants, and bogs allows for examination and manipulation across a variety of spatial scales (Kneitel and Miller 2003). Additionally, the species that inhabit pitcher plant leaves are unique to the plant and have relatively short generation times (hours to weeks); such a life history allows for short experiments that encapsulate the dynamics of this system (Kneitel and Miller 2003).

Pitcher plants have been featured previously in the discussion of metacommunity theory (Miller and Kneitel 2005). Dispersal is important to the pitcher plant; studies have demonstrated that dispersal rates significantly affect inquiline community composition (Miller et al. 2002; Kneitel and Miller 2003). In fact, in the absence of dispersal, inquiline richness is low due to

extinction caused by predation and competition (Kneitel and Miller 2003). However, studies have yet to follow migration from source to destination, and virtually no experimental evidence addresses the actual dispersal distances of inquilines (Miller and Kneitel 2005). Furthermore, it is unclear whether migration is a “declining function of distance between leaves” or whether it is “best represented as a lottery in which species colonize pitchers from a large pool (air)” (Miller and Kneitel 2005). As such, in order to better understand pitcher plants in the context of metacommunity theory, inquiline modes and ranges of dispersal must be determined.

The purpose of this study is to evaluate the degree to which pitcher plant isolation affects the diversity of the community that colonizes it. Because inquiline dispersal distances are unknown, this study will attempt to determine whether maximum dispersal distances lay within the range of 0 to 5 m. The specific hypothesis being tested is that inquiline diversity will decline as plant isolation increases, as projected by island biogeography theory.

MATERIALS AND METHODS

Natural history of the community

The purple pitcher plant is a carnivorous plant found in low-nutrient wetlands and bogs across North America, from the southeastern United States, up through Canada, and as far west as British Columbia (Miller and Kneitel 2005). In its northern range, the pitcher plant primarily grows in sphagnum-peat bogs (Cody and Talbot 1973; Naczi *et al.* 1999).

Individual plants contain multiple leaves or “pitchers”; in our experimental area, some contained as many as fifteen (pers. observ.). These leaves can hold between 0 and 50 mL of rainwater (Miller and Kneitel 2005), forming an aquatic habitat for a suite of organisms on which the plant depends (Bradshaw and Creelman 1984). The plant’s primary source of nutrients is

invertebrate prey that may be attracted to nectar or leaf coloration, falls into the pitcher, and drowns (Miller and Kneitel 2005). The prey, which consists largely of ants (Heard 1998), is decomposed by bacteria or consumed directly by detritivores such as mites and midges, in particular the pitcher plant mite (*Sarraceniopus gibsoni*) and pitcher plant midge (*Metriocnemus knabi*) (Capinera 2008). The middle trophic level consists of protozoa and a few species of rotifers, notably *Habrotrocho rosa*, which feed on the bacteria (Kneitel and Miller 2003). Over 40 species of protozoa, and many more of bacteria, have been found in pitcher plant phytotelmata (Capinera 2008). The top predator is the larva of the filter-feeding pitcher plant mosquito (*Wyeomyia smithii*), which subsists on protozoa, rotifers, and occasionally bacteria (Heard 1994). Another notable inquiline includes the flesh fly (*Fletcherimyia fletcheri*) (Capinera 2008).

Inquiline species colonize leaves on a time scale of hours to weeks (Judd 1959; Kneitel and Miller 2003). Very little is known about the mechanisms of natural dispersal and the origins of dispersers, but modes likely vary for each species (Miller and Kneitel 2005). Bacteria and protozoa, for example, may occur in soils or open waters in the area and disperse as propagules carried in the air (Maguire 1963; Miller and Kneitel 2005). Others, including the pitcher plant mosquito, the pitcher plant midge, and the pitcher plant flesh fly, are obligate inquilines of pitcher plants and most likely colonize from nearby leaves. While the mosquito can disperse as an adult, the midge and flesh fly may crawl from pitcher to pitcher (Miller and Kneitel 2005).

Experimental Design

This study was conducted in a population of *S. purpurea* at Forest Service Bog at the University of Notre Dame Environmental Research Center in the Upper Peninsula of Michigan (UNDERC, 46° 13' N by 89° 32' W). Forest Service Bog is a sphagnum-dominated bog

surrounded by a new-growth forest undisturbed since logging up to 80 years ago (Vogelheim 2007). This particular site was chosen for its abundance of pitcher plants and ease of accessibility to said plants.

Ten pairs of pitcher plants were used in this study. Forty-six viable plants were identified in the field based on the following criteria: the plant had between seven and fifteen pitchers, all pitchers were of approximately the same size, and the leaves were green or dark red, not desiccated, and without holes or evidence of grazing. These 46 plants spanned the circumference of Forest Service Bog. Ten were chosen as the “target pitcher plant” (i.e. the plant to be flushed out and recolonized) using a random number generator; ten others were chosen from the remaining 36 to function as the “source” plant (i.e. the plant to colonize the target plant).

Distances between source and target plants ranged from 0 to 5 m: 0.2, 1.4, 1.4, 1.8, 2.1, 2.6, 3.1, 3.5, 4.1, and 5 m. All other plants within a 5 m radius of the target plant were covered with gardening tarp and nails to prevent them from colonizing the target plant (Fig. 1). A distance of at least 10 m separated all target-source pairs, ensuring that no pair confounded another.

Three leaves from each target and source plant were randomly selected and notched on the hood so that the same pitchers were sampled at 1-week intervals over the course of the study. The remaining leaves of the plant were covered with gardening tarp and secured with a rubber band to prevent “intracolony” within the plant (Vogelheim 2007).

Field Sampling

The experiment began on June 17, 2010. For each water-bearing leaf of the target plants, a sterile plastic pipette was used to mix, remove, and place the entire contents into a labeled sterile 120 mL plastic cup. At this time, the target pitchers were empty. In the laboratory, the

pitcher contents were vacuum-filtrated using 0.7- μ m filter paper to isolate the pitcher fluid from inquilines and other detritus.

In the field on June 21, 2010, 20 mL of filtered pitcher fluid was returned to the appropriate leaves of the target plants; 20 mL was chosen because it was the average volume of liquid found in the target plant leaves. Subsamples (0.3 mL) from the notched pitchers of the source plants were pipetted into sterile labeled plastic microcentrifuge tubes. The inquiline diversity of these samples was later evaluated in the laboratory. Subsampling (0.3 mL) of the target plants occurred each week for three weeks for a total of 90 samples.

Species identification and enumeration

The abundance of invertebrates (including rotifers) and protozoa was determined. Bacteria were not quantified in this study due to difficulty and time constraints. Individuals were counted in a standard subsample (0.1 mL) using a Palmer cell counter and a compound microscope (x100) (Buckley et al. 2004). Individuals were identified to genus when possible (Pennak 1989; Covich and Thorp 2001). In addition to referencing texts, I consulted David Hoekman and Jamie Kneitel via email, both of which have experience with pitcher plants and their inquilines. It should be noted, however, that protozoa were difficult to differentiate for a novel observer.

Statistical Analysis

The diversity of each pitcher subsample was determined using the Shannon-Wiener Index (Shannon 1948), among the most common measures of diversity. A simple linear regression was conducted in which distance between each source and target pitcher was the independent variable and inquiline diversity was the dependent variable. Species richness was calculated as

the number of distinct taxa present. A second regression between dispersal distance and inquiline richness was performed.

When preliminary analysis revealed that isolation and diversity were not related, data from all pitcher plants was pooled and used to evaluate richness as a function of time. Richness was transformed by raising it to the fourth power; this was the lowest exponent at which the data conformed to a linear trend. A third regression between richness and time was performed. All statistical analysis was conducted using SYSTAT 13.

RESULTS

Over the course of the experiment, all pitchers remained intact (there were neither holes nor signs of damage). In the fluid collected from pitchers, five invertebrate species and four protozoan taxa were encountered. These included the pitcher plant mosquito (*Wyeomyia smithii*), midge (*Metriocnemus knabi*), sarcophagid (*Fletcherimyia fletcheri*), mite (*Sarraceniopus gibsoni*), a bdelloid rotifer (*Habrotrocha rosa*), as well as the following protozoan taxa: colpoda, cyclidium, cryptomonas, and bodo. Pitchers contained between zero and nine taxa (mean=5).

Regression analysis indicated that there was no significant relationship between dispersal distance and inquiline diversity at any sampling period (Table 1). Additionally, there was no significant relationship between dispersal distance and inquiline richness (Table 2 and Fig. 2). In fact, both relationships were weakly *positive*, contrary to what we would expect.

All nine taxa observed during the study appeared in all target plants by the end of the first week, regardless of distance between target and source plants. Additionally, 6.7% of the time, an individual was observed in the target plant that was not observed in the source plant at the time the experiment began (i.e. at time zero).

Abundance of each of the four protozoan taxa observed showed an increasing trend with time; statistics describing this relationship were challenging because of low sample size. There was no consistent trend with invertebrate abundance and time. Time and inquiline richness were significantly and positively correlated ($r^2=0.992$, $F_{0.05,1,2}$ $P=0.004$) (Fig. 3). Most of this increase in richness occurred by the end of the first week (79.8%).

DISCUSSION

The original intent of this study was to elucidate the relationship between dispersal distance and inquiline diversity within communities of purple pitcher plants. I expected to see inquiline diversity decline with increasing pitcher isolation; theoretically, as the distance between source and target habitats increases, fewer dispersing individuals should successfully reach the target habitat by chance (MacArthur and Wilson 1963). However, there was no relationship between these two variables.

The most likely explanation is that the range of distances employed in this study is well within the maximum dispersal capacity of the inquiline taxa observed. The fact that inquiline diversity did not vary with plant isolation, as well as the fact that all taxa appeared in (i.e. successfully reached) all target plants substantiates this conclusion. Protozoa in particular are not likely limited by a 5 m range; protozoan cysts have been found in the air and are subject to the wind. Evidence suggests that they disperse and recolonize with the help of rain, which removes cysts from the air column (Maguire 1963). In regards to the nature and range of aquatic invertebrate dispersal, experimental studies provide conflicting evidence; these organisms may not even be dispersal limited (Maguire 1963; Cáceres and Soluk 2002). Findings from this particular study suggest that the invertebrates that inhabit pitcher plants (e.g. the mosquito,

midge, mite, and flesh fly) are not limited by dispersal on the order of 5 m. It ought to be noted again that mechanisms of inquiline dispersal are still poorly understood (Miller and Kneitel 2005); such a conclusion would be stronger with more empirical evidence.

A number of other plausible explanations may account for the lack of relationship between pitcher isolation and inquiline diversity in this particular study. To begin, the radius (5 m) at which all plants surrounding the target plant were covered with gardening tarp may not have been large enough; plants just outside this radius may have acted as disperser sources. Furthermore, the tarp may not have been an effective material or method by which to preclude these plants as source populations. The midge and flesh fly, for example, could have crawled out from beneath the tarp to colonize the target plant. The fact that taxa absent from source plants were found in target plants supports this conclusion. Second, the life cycle of individual taxa was not taken into account in experimental design and implementation. For example, the pupation and emergence of adult midges, mosquitoes, and flesh flies, which occurs in mid-summer, could have influenced the diversity of the communities observed (Berry 2003). Additionally, high reproductive rates in protozoa, for example, could increase abundances observed, particularly at later sampling times. This, in turn, would affect the Shannon diversity index, a measure that depends upon both richness and evenness. A more robust study would intentionally choose a time of year and time-scale over which to sample, such as after the pupation of dipterans or over a much shorter period of time than three weeks. Third, the natural addition of allochthonous material has been shown to affect the composition and diversity of inquiline communities from the bottom-up (Cochran-Stafira and von Ende 1998; Kneitel and Miller 2002). This was not controlled for in this study (i.e. all plants were not covered to prevent introductions) and may have confounded results. Finally, leaf age and leaf morphology (such as leaf length and volume)

have also been shown to affect inquiline diversity (Miller and Kneitel 2005). Plants were selected in this study based on the *appearance* of equal size (i.e. size was not actually measured and quantified). Ultimately, it may be unrealistic to expect dispersal distance alone to have a significant impact on the diversity within a particular pitcher plant; a suite of other factors can shape local diversity.

Because pitcher isolation was not shown to have an effect on inquiline diversity, I justified pooling together data from all target plants to evaluate how richness varied with time. A positive relationship was observed; it appears that as more time is allowed for inquilines to disperse to emptied plants, the more species can colonize, a relationship previously demonstrated by a number of empirical studies (e.g. MacArthur and Wilson 1963; Caceres and Soluk 2002). It is important to note, however, that such a conclusion would have been stronger with more observations.¹ To more accurately evaluate the relationship between richness and time, I would suggest taking samples on a more frequent basis for a period no less than three weeks as previous studies have shown that recolonization of pitchers can take place on the order of hours to days (Judd 1959). Although it was not the original intent of this study to look at colonization over time, the appearance of a trend is evidence that further investigation may be worthwhile.

CONCLUSION

It became clear that efforts to answer my original research question (i.e. how inquiline diversity varies as a function of dispersal distance) were premature; a better understanding of the nature of purple pitcher plant inquiline dispersal—mechanisms, rates, and natural distances—is necessary before a similar study is attempted in the future. Such information would inform both

¹ My original question did not require me to sample frequently and intermittently as inquiline communities reached stable and natural compositions, a process that takes approximately 2-3 weeks (Miller *et al.* 1994). Thus, I subsampled only three times over the course of three weeks.

experimental design as well as the creation of computer models that simulate inquiline colonization.

To determine the range of dispersal distances of which pitcher inquilines are capable, a much broader range of distances ought to be manipulated, perhaps as great as 100 m. This might require removing entire plants from the bog and placing them, potted, outside the range of bog. Such a study should explore more effective ways of isolating target and source plants, perhaps by removing all confounding plants entirely. This study should also sample more frequently, particularly in the first week after the target plants are flushed out, and many more pitcher plants to increase sample size. In addition to an *in situ* study, an experiment carried out in a greenhouse with potted pitcher plants (i.e. removed from the bog) might be useful to compare to observations in the field. This would help better isolate target and source pairs from all other confounding pitcher plants. Such an experimental design would enable an evaluation of the *rates* at which pitcher plant inquilines are capable of dispersing; one would simply note the time at which particular taxa appear in target plants. One must try to take into account, however, the fact that taxa with high reproduction rates may affect the abundance observed.

Because communities associated with *Sarracenia purpurea* yield results applicable to other community types (particularly members of other phytotelmata) (Miller and Kneitel 2005), studies like those proposed above are worthwhile. As our knowledge of the processes that influence metacommunities grows, we can continue to understand and explain the diversity observed on multiple spatial scales.

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Table 1. Results from a simple linear regression illustrating the relationship between dispersal distance and inquiline diversity. Diversity was quantified using Shannon-Wiener's index. No significant relationships were found.

	r^2	$F_{0.05,1,8}$	P-value
<i>Week 1</i>	0.270	2.965	0.123
<i>Week 2</i>	0.200	1.996	0.195
<i>Week 3</i>	0.239	2.515	0.151

Table 2. Results from a simple linear regression illustrating the relationship between dispersal distance and inquiline richness. No significant relationships were found.

	r^2	$F_{0.05,1,28}$	P-value
<i>Week 1</i>	0.270	2.278	0.142
<i>Week 2</i>	0.160	5.351	0.028
<i>Week 3</i>	0.026	0.740	0.397

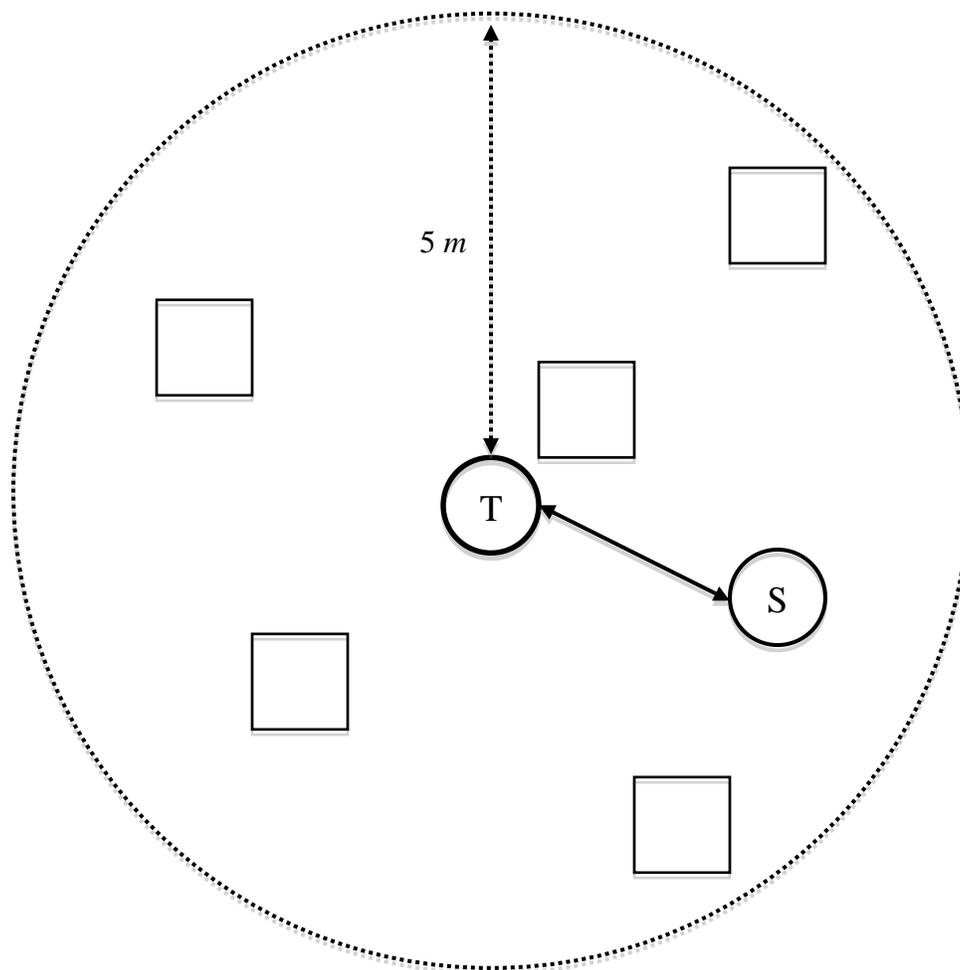


Figure 1. *Diagram of experimental plot utilized in this study.* Ten such experimental plots were employed. The circle labeled “T” represents the target pitcher plant; the circle labeled “S” represents the source pitcher plant. The distance between target and source plants varied between 0 and 5 m, represented here as an unlabeled solid arrow. Black squares represent pitcher plants within the 5 m radius of the target plant that were covered with gardening tarp. Figure not drawn to scale.

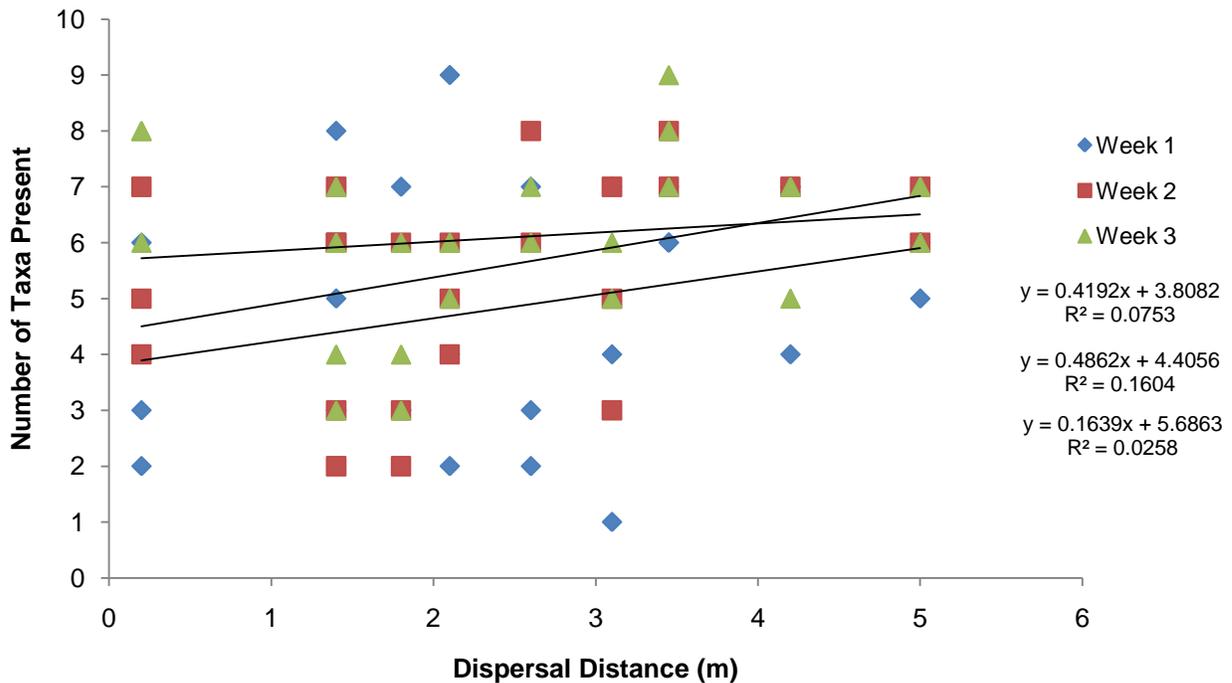


Figure 2. Number of species present within target pitchers sampled at the end of each week represented as a function of dispersal distance. Each target plant was separated from a source plant by a distance ranging from 0.2 to 5 m. Each target plant was sampled one, two, and three weeks after target pitchers were flushed, filled with filtered pitcher fluid, and permitted to recolonize. No significant relationship between dispersal distance and inquiline richness was determined for any of the weeks sampled (Table 2).

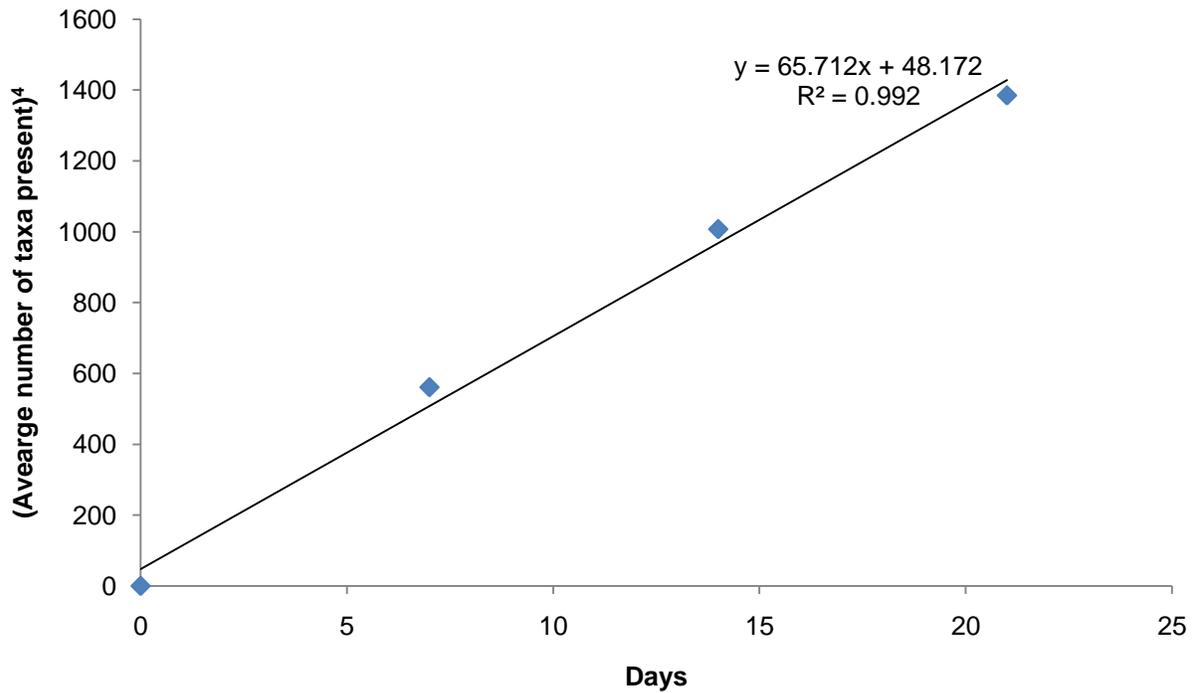


Figure 3. Colonization curves of 10 pitcher plants at Forest Service Bog over a three-week period. Inquiline richness (\pm SE), transformed to the fourth power, is shown as a function of time since the target pitchers were flushed out, filled with filtered pitcher fluid, and permitted to recolonize ($r^2=0.992$, $F_{0.05,1,2}$ $P=0.004$).