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Carnivorous pitcher plants eat a diet of certain spiders, regardless of what's on the menu

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Abstract. The purple pitcher plant, *Sarracenia purpurea*, is a low-lying carnivorous plant that uses pitcher-shaped leaves to catch arthropod prey for nutrition. Spiders make up a significant portion of these prey. To determine the tendency of specific spider taxa to be captured by the plant, we compared the composition (by taxonomic family) of three spider assemblages: those captured by the plant, those residing on or over the plant, and those found nearby in the local environment. Although there were some broad similarities within the three spider assemblages, significant differences existed when specific families and guilds were considered. While some families (e.g., Linyphiidae and Lycosidae) and guilds (e.g., low sheet/tangle weavers) were heavily represented in all three assemblages, other groups varied, and we found that the taxonomic makeup of victimized and resident spiders did not always reflect their environmental abundances. Moreover, spider assemblages captured by *S. purpurea* were extremely similar across distant locations regardless of environmental spider assemblage composition, suggesting that *S. purpurea* is very selective in its spider capture regimen.

Key words: assemblages; carnivorous plant; plant–insect interactions; predator–prey relationship; *Sarracenia purpurea.*

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INTRODUCTION

Carnivorous plants capture a great diversity of prey, including spiders, for nutrient supplementation. However, due to the trophic similarity between spiders and carnivorous plants as predators of insects, the ecological relationship between these organisms is complex. Spiders often fall victim to carnivorous plants (Wray and Brimley 1943, Ellison and Gotelli 2009), yet may also act as resource parasites when they steal prey from sticky leaves (Anderson and Midgley 2002) or live inside pitchers as residents and potentially intercept prey intended for the plant (Cresswell 1993).

The purple pitcher plant, *Sarracenia purpurea*, is a low-lying herbaceous perennial that uses pitcher-shaped leaves to capture mostly arthropod prey (Schnell 2002). Common prey of *S. purpurea* include insects, spiders, harvestmen, mites, mollusks, and the occasional small vertebrate (Lloyd 1942, Wray and Brimley 1943, Judd 1959, Cresswell 1991, Heard 1998). Nectaries and pigmented lines may be used by *S. purpurea* to capture these prey (Juniper et al. 1989, Plachno 2007, Schaefer and Ruxton 2008, Bennett and Ellison 2009), although recent evidence points to the presence of nectar rather than pigment (Green and Horner 2007, Bennett and Ellison 2009) as the defining difference between the capture rate of a *S. purpurea* pitcher vs. a cup in the ground (e.g., a pitfall trap). The main difference between new and old pitchers is the greater amount of nectar produced by new pitchers (Fish and Hall 1978, Bennett and Ellison 2009) along the lip of the pitcher and along pigmented lines (Schnell 2002), and newer pitchers

are often more effective at capturing prey than older ones (Wolfe 1981). Moreover, spiders often consume nectar (Nyffeler et al. 2016), and they may fall victim to the plant via the serendipitous discovery of nectar and entrapment the same way that prey insects do, as is suggested to occur with other carnivorous plants (Williams 1976, Zamora 1995).

Only a few studies have examined the ecological interactions between spiders and *S. purpurea*, and most have focused on the morphological features such as nectaries and pigmentation rather than the surrounding prey community. For example, physical features, such as the size and height of the pitcher, have been shown to affect the rate of spider residency near *S. purpurea* (Cresswell 1993), but the presence of nectar or pigment does not (Milne and Waller 2013). In addition, it has been shown that some spiders readily drink nectar that is similar in composition to *S. purpurea* nectar (Cipollini et al. 1994, Pollard et al. 1995, Deppe et al. 2000, Amalin et al. 2001, Jackson et al. 2001, Taylor 2004, Nahas et al. 2016). Spiders have also been observed to use *S. purpurea* pitchers (Jones 1935, Milne 2012) and seed heads (Jennings et al. 2008) as oviposition sites.

Although spiders have long been known to be common prey of *S. purpurea*, no studies have compared visitors and/or prey capture of *S. purpurea* to their local abundance. For example, Wray and Brimley (1943) studied the efficacy of spider capture by the plant but limited their examinations to only the spiders that were captured, ignoring the surrounding spider fauna. Other researchers studying this phenomenon have lamented the lack of data on the local arthropod fauna near *S. purpurea* populations and note that the inclusion of such data would allow for insights into the differences in prey capture among spatially separated *S. purpurea* populations (Heard 1998). In addition, such data could reveal if *S. purpurea* pitchers act as pitfall traps that catch a random subset of the surrounding spider assemblage, or selectively catch certain spider taxa. Additionally, different groups or guilds of spiders may differ in their habits, including their tendencies to live above, beside, or inside carnivorous plants as web-building residents.

Objectives of the current study were to compare spider biodiversity captured within the pitchers of *S. purpurea* to the spider community in the surrounding ecosystem. Additionally, the spider assemblage captured by the plant was compared to spiders found living over or in the pitchers (henceforth, "residents") to determine whether they were also commonly victims.

Methods

Field-sites

The spiders within three pitcher plant populations at three sites were sampled: Blackwater Ecological Preserve (BEP), Joseph Pines Preserve (JPP), and Highlands Biological Station (HBS). Both BEP (36.87° N, 76.83° W; 319 acres) and JPP (37.05° N, 77.24° W; 120 acres) are in eastern Virginia (approximately 50 km away from each other), while HBS is located in western North Carolina (35.05° N, 83.19° W; 11 acres; 610 and 579 km from BEP and JPP, respectively). Blackwater Ecological Preserve and JPP are fire-dependent communities dominated by turkey oak (*Quercus laevis*) and loblolly pine (*Pinus taeda*), with many herbaceous shrubs and open spaces with low-lying plants (Frost and Musselman 1987), whereas the sampled region of HBS was a botanical garden on the edge of a lake. Blackwater Ecological Preserve has approximately 15–25 naturally occurring *S. purpurea* plants, whereas JPP is an artificially managed location, manipulated to have bogs and swales with approximately 75 *S. purpurea* plants planted in 2003. Although HBS is the smallest of all three sites, it has the largest population of *S. purpurea* with approximately 700 pitcher plants. The genetic relationships among the plants within each population were unknown and not tested. Both BEP and JPP are subjected to prescribed burns at least once a year.

Captured composition

To quantify the spider assemblage that was captured by *S. purpurea*, the composition of captured prey was examined at all three locations (henceforth, "CC" for "captured composition"). At BEP, five randomly selected pitchers from 20 plants were sampled for captured spiders approximately every other month for ten months (n = 600; September 2006–June 2007). At HBS, two randomly selected pitchers from 50 plants were sampled four times over two months (n = 400; June 2007–July 2007). At JPP, three randomly selected pitchers from seven plants and one

randomly selected pitcher from 25 other plants were sampled every month for six months (n = 276; April 2008–September 2008). Pitchers were sampled only once per season. To ensure similar collection ability, only pitchers from the current growing season were sampled. To ensure that pitchers were not sampled twice, pitchers were given a small mark with a black permanent marker to distinguish them from unsampled pitchers. Pitchers were sampled by first removing and discarding all liquid and associated prey using a turkey baster and smaller plastic pipettes. Pitchers were then filled half-full of distilled water. After one week, all prey were removed from the pitchers and preserved. Spiders were separated from other prey, preserved in 80% ethanol, sexed, checked for maturity, and identified to species using Ubick et al. (2017) and other taxonomic keys.

Spider residents

Spiders found crawling on the pitcher plant or in a web that was attached to a pitcher plant ("residents"; henceforth, "RES") were collected. Plants were sampled for residents by hand with the aid of a manual glass vial aspirator (Model no. 1135B, Glass vial aspirator, Bioquip Products, Rancho Dominguez, California, USA), or electronic aspirator (Model no. 2820A, AC Insect Vacuum, Bioquip Products). Residents were collected once a month for one year at BEP from all 22 plants (n = 264), once a week over two months on approximately 130 randomly selected plants at HBS (n ≈ 1040), and once a month over six months on 32 randomly selected plants at JPP (n = 192). Spiders were preserved, analyzed, and identified as above.

Spiders in the surrounding environment (SN + SB + PT)

To sample the surrounding spider population, 25-m^2 plots were created surrounding pitcher plants at each site. Five plots were created at BEP, two at HBS and three at JPP. Variable plot numbers were required due to either limited space (HBS) or limited regions with grouped pitcher plants (JPP). Each plot was sampled for spiders using three techniques: sweep netting (SN), shrub beating (SB), and pitfall trapping (PT). Spiders captured using these techniques (SN + SB + PT) were considered spiders from the environment (ENV). These techniques were conducted once every other month for one year at BEP and four times over two months (June–July) at HBS. At JPP, PT was conducted once a month over six months (April–September), while SN was done once every other month for six months (April–September; SB was not conducted at JPP due to the lack of tall shrubs). Sweep netting consisted of waving a sweep net (0.5 m diameter) over grassy vegetation. Four sweeps per 1-m^2 section of each plot were conducted. Foliage and plants that were too large to be sampled by SN were sampled with a 71-cm^2 beating sheet. Foliage was considered eligible for SB if it had a height of >0.25 m and a bole width of <3 cm in diameter. Foliage that had a bole width of >3 cm in diameter was considered a tree and not sampled. Beating sheets were placed on the ground below each shrub and the shrub was shaken 10 times over the sheet. Pitfall trapping consisted of using 147.9-mL (5 oz) cups filled half-full of soapy water. Each pitfall trap was placed in the ground, flush with the forest floor. Five pitfall traps were established in each plot. Four of the five pitfall traps were placed at approximately 1 m from each corner of the plot and the fifth pitfall trap was placed at the center of each plot. After one week, the pitfall traps were collected. For all techniques, all spiders were preserved, analyzed, and identified as above.

Statistical methods

Comparisons among spider taxa were done at the family, genus, and species levels. Multiple analyses were conducted because most spiders (68%) could not be identified to genus or species due to being immature (developed genitalia are usually necessary for genus and species determination) and therefore sample sizes were drastically reduced when analyzing these data at lower taxonomic levels. However, similar studies of spider diversity have successfully used the family level for their analyses (Whitmore et al. 2002, Shochat et al. 2004). In addition, spiders were placed into guilds based on family according to the guilds proposed by Uetz et al. (1999) with some slight modifications. These guilds were as follows: foliage runners (Anyphaenidae, Clubionidae, Corinnidae, and Miturgidae), ground runners (Lycosidae and Gnaphosidae), stalkers (Oxyopidae and Salticidae), ambushers (Thomisidae, Philodromidae, and Pisauridae), sheet web-builders (Agelenidae, Cybaeidae, and Hahniidae), low sheet/tangle

weavers (Linyphiidae, Mysmenidae, and Theridiosomatidae), orb weavers (Araneidae and Tetragnathidae), and space web-builders (Theridiidae, Dictynidae, and Pholcidae). Mygalomorph spiders (we only captured two) were not used for this analysis.

Shannon–Wiener diversity indices were calculated for each capture technique at the family, genus, and species level. Comparisons among capture methods of their Shannon–Wiener diversity indices—at the family, genus, or species level—were conducted using three separate ANOVAs. Tukey honestly significant difference (HSD) post hoc tests were conducted if significant *P*-values were revealed.

For RES and CC, statistical replicates were created by dividing the plants within each location into four similarly sized groups that were spatially near each other. For SN + SB and PT, statistical replicates were the individual plots per location.

The similarities among taxonomic communities at each taxonomic level and among guilds were compared using separate non-metric multidimensional scaling (NMDS) analyses in R (R Development Core Team, 2018) version 3.4.3 and the associated vegan package. This technique was used to compare the taxonomic makeup of the spider community captured through (1) CC vs. those captured on the plant (RES) vs. those found in the environment (ENV) and (2) CC vs. SN + SB vs. PT vs. RES. Significance between specific capture methods (e.g., CC vs. SN + SB within NMDS #2) was determined using the pairwise.adonis function in R (Martinez 2017). *P*-values were adjusted within this pairwise.adonis function using a Bonferroni correction. Plots were created using R with the associated ggplot2 package.

Prior to each NMDS, data were standardized; for instance, CC and RES data were divided by the number of sampling time units multiplied by the number of plants sampled for each collection type. Furthermore, PT and SN + SB data were divided by the number of sampling time units multiplied by the number of plots sampled for each collection type. Data were then square-root-transformed prior to each NMDS.

Results

Throughout the study, 1727 spiders were captured and identified. Of that number, 1622 were able to be placed into taxonomic families and used for data analysis. The number of spiders captured in each guild and family is reported in Table 1. Victims of *S. purpurea* (CC) were most often sheet web-spiders (Linyphiidae) and wolf spiders (Lycosidae), which largely reflected the proportions of spiders found as residents (Table 2). However, in the surrounding environment (SN, SB, and PT), these families were reduced in their proportional collection rate. Other groups of spiders (e.g., Salticidae, Araneidae, and Thomisidae) were more common in the environment than as victims or as residents (Table 2). Some spider families that were present in the environment (e.g., hahniids) or as residents (e.g., agelenids), or both (e.g., pisaurids) were never, or very rarely, captured by pitchers (Table 2). The most commonly collected species were *Pirata insularis* (Lycosidae), *Ceratinopsis laticeps* (Linyphiidae), *Tenuiphantes sabulosus* (Linyphiidae), *Ceratinopsis interpres* (Linyphiidae), and *Varacosa avara* (Lycosidae; see Appendix S1 for full species list).

When analyzed at the genus ($F_{3,40} = 0.05$; $P = 0.99$) and species level ($F_{3,40} = 0.14$; $P = 0.99$), there was no significant difference found among spider assemblages by capture technique. However, when analyzed at the family level, the spider assemblage captured by pitcher plants (CC) was significantly different from that which was found in the environment (ENV; $F_{1,20} = 32.77$; $P < 0.005$) and from that which was found near or crawling on the plant (RES; $F_{1,22} = 4.251$; $P < 0.05$; Fig. 1). Additionally, the spider assemblage captured by pitchers (CC) was significantly different from that which was found in pitfall traps alone (PT; $F_{1,20} = 30.512$; $P < 0.005$; Fig. 1). Moreover, the taxonomic makeup of the spider assemblage that was captured by *S. purpurea* (CC) was very similar across the three locations. In fact, these captured assemblages (CC) were more taxonomically similar to each other than to any other spider assemblage (Fig. 1).

There was a significant difference among the spider assemblages captured by each technique when they were organized by guild ($F_{3,40} = 23.33$; $P < 0.0001$; Table 3). In post hoc pairwise tests, each comparison of capture technique was significantly different from the other (RES vs. SN + SB: $F = 21.63$, $P < 0.005$; RES vs. CC: $F = 3.74$, $P < 0.05$; RES vs. PT: $F = 20.59$, $P < 0.005$; SN + SB vs. CC: $F = 22.96$, $P < 0.005$; SN + SB

Table 1. Number of spiders captured by family and guild.

Family	Number found	Guild assignment	Guild	Number found
Agelenidae	29	Sh	Ambushers (A)	88
Anyphaenidae	2	F	Foliage runners (F)	23
Araneidae	87	O	Ground runners (G)	456
Atypidae†	1	N/A	Low sheet/tangle weavers (L)	635
Clubionidae	7	F	Orb weavers (O)	101
Corinnidae	10	F	Sheet web-builders (Sh)	51
Ctenizidae†	1	N/A	Space web-builders (Sp)	53
Cybaeidae	8	Sh	Stalkers (St)	215
Dictynidae	3	Sp		
Gnaphosidae	44	G		
Hahniidae	19	Sh		
Linyphiidae	630	L		
Lycosidae	412	G		
Miturgidae	4	F		
Mysmenidae	3	L		
Oxyopidae	18	St		
Philodromidae	3	A		
Pholcidae	1	Sp		
Pisauridae	26	A		
Salticidae	197	St		
Tetragnathidae	14	O		
Theridiidae	44	Sp		
Theridiosomatidae	2	L		
Thomisidae	59	A		

† Mygalomorph spiders ($n = 2$) were excluded from guild assignments.

Table 2. Percentage of families of spiders collected with all techniques.

Family	Environment (%)	CC (%)	RES (%)
Agelenidae	0.12	0.37	5.26
Araneidae	8	1.48	3.12
Clubionidae	0.24	1.48	0.2
Corinnidae	0.48	1.85	0.2
Dictynidae	0.71	0.37	0.2
Gnaphosidae	2.61	7.41	0.39
Hahniidae	1.54	0.37	0
Linyphiidae	30.8	41.5	50.5
Lycosidae	23.3	27.8	27.5
Oxyopidae	1.54	0.74	0.59
Pisauridae	1.9	0	1.95
Salticidae	18.2	11.1	2.73
Tetragnathidae	0.6	0.37	1.56
Theridiidae	2.38	1.48	3.9
Thomisidae	6.06	2.22	0.4
Other	1.52	1.46	1.5

Notes: "Other" includes Anyphaenidae, Atypidae, Ctenizidae, Cybaeidae, Liocranidae, Miturgidae, Mysmenidae, Philodromidae, Pholcidae, and Theridiosomatidae. Environment (SN + SB + PT); CC, captured composition; PT, pitfall trapping; RES, residents; SB, shrub beating; SN, sweep netting.

vs. PT: $F = 17.42$, $P < 0.005$; CC vs. PT: $F = 37.75$, $P < 0.005$; Fig. 1). These significant differences were also present when spider assemblages organized by guild found in CC and RES were compared with those found in the environment (SN + SB + PT; $F_{2,31} = 35.085$; $P < 0.0001$). In post hoc pairwise tests, each comparison of capture technique was also significantly different from the other (RES vs. CC: $F = 3.586$, $P = 0.035$; RES vs. ENV: $F = 31.85$, $P < 0.005$; CC vs. ENV: $F = 47.67$, $P < 0.005$; Fig. 1).

The Shannon–Wiener diversity indices of spider assemblages organized by family ($F_{3,40} = 1.9$; $P = 0.15$) and genus ($F_{3,40} = 1.6$; $P = 0.20$) were not significantly different among capture techniques. However, when organized by species, these Shannon–Wiener diversity indices were significantly different ($F_{3,40} = 3.15$; $P < 0.05$) among capture techniques. In a post hoc Tukey HSD test, it was shown that SN + SB was significantly less diverse than PT ($F = 3.33$; $P < 0.0001$).

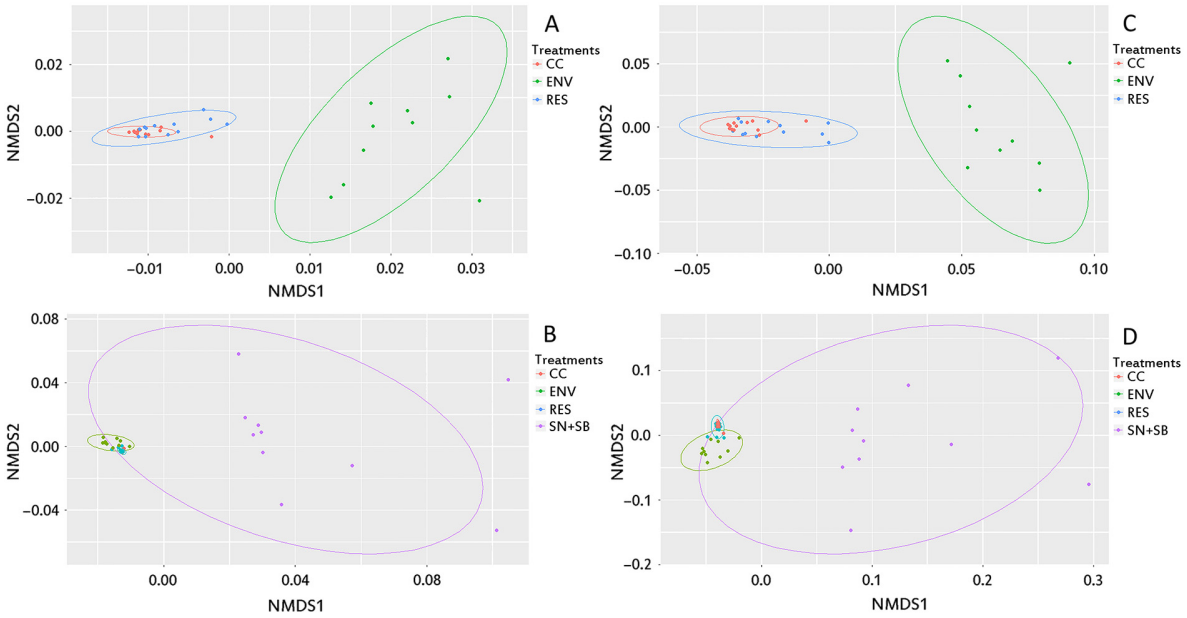

Fig. 1. Plots of non-metric multidimensional scaling analyses of various treatment comparisons at the family and guild levels. Ellipses represent 95% confidence intervals. (A) A comparison of the spider assemblages organized by family captured by *Sarracenia purpurea* (captured composition [CC]) vs. those sampled over or on the plant (residents [RES]) vs. those sampled from the surrounding environment (SN + SB + PT; ENV); (B) a comparison of the spider assemblages organized by family captured by CC vs. those sampled by sweep netting and shrub beating (SN + SB) vs. RES vs. those sampled from pitfall traps nearby (PT); (C) a comparison of the spider assemblages organized by guild captured by CC vs. RES vs. ENV; (D) a comparison of the spider assemblages organized by guild captured by CC vs. SN + SB vs. RES vs. PT.

Table 3. Percentage of spiders within guilds captured through each technique (N).

Guild	RES	SN + SB	CC	PT
Ambushers	2.34% (12)	13.5% (52)	2.96% (8)	3.53% (16)
Foliage runners	0.78% (4)	1.30% (5)	3.70% (10)	0.88% (4)
Ground runners	27.9% (143)	2.59% (10)	35.2% (95)	45.9% (208)
Orb weavers	4.68% (24)	17.4% (67)	1.85% (5)	1.10% (5)
Sheet web-builders	5.85% (30)	0.26% (1)	1.11% (3)	3.75% (17)
Space web-builders	4.09% (21)	5.18% (20)	1.85% (5)	1.55% (7)
Stalkers	3.31% (17)	34.2% (132)	11.9% (32)	7.51% (34)
Low sheet/tangle weavers	51.1% (262)	25.7% (99)	41.5% (112)	35.8% (162)

Notes: CC, captured composition; PT, pitfall trapping; RES, residents; SB, shrub beating; SN, sweep netting.

Discussion

When examined at the family level, the spider assemblage captured by *S. purpurea* (CC) was significantly different than that of the local community; for instance, araneids (orb weavers) were less commonly found as prey than their environmental abundance would suggest, most likely due to their behavior of building vertical webs placed high (20–70 cm off the ground; Foelix 2010) typically well above the height of *S. purpurea* pitchers. Pisaurids (nursery web spiders and fishing spiders) were rarely captured but had high abundances in the environment. This may be due to the unique ability of many pisaurids (e.g., *Dolomedes*) to dive into and walk

on top of water (McAlister 1960), thereby avoiding capture if they did fall into pitchers. Other families of spiders, such as gnaphosids and linyphiids, were more commonly found as victims. Although it is unknown why gnaphosids were often victims, the high capture rate of linyphiids may be due to their tendency to build horizontal webs at approximately the same height as *S. purpurea* pitchers (~4 cm off the ground; Sunderland et al. 1986). Moreover, some linyphiids were observed in webs inside *S. purpurea* pitchers, a phenomenon that makes sense when coupled with the fact that many smaller linyphiid spiders build webs of 4–8 cm^2 (Sunderland et al. 1986, Harwood et al. 2001) in size, a range similar to the mean web area inside a random sampling of *S. purpurea* pitchers (7.69 cm^2; M. A. Milne, *unpublished data*). These smaller linyphiids that reside inside pitchers may easily become prey due to slips along the smooth inner surface of the pitcher while attempting to build their webs. Indeed, these smaller linyphiids often hunt for prey at the edges of their web (Harwood et al. 2003), which may have contributed to accidental falls into the pitcher depths. Other factors, such as the consumption of nectar along the inner pitcher walls (Nyffeler et al. 2016), may also explain the higher incidences of linyphiid captures by pitchers. Although many other groups of spiders also consume nectar (Nyffeler et al. 2016), because the webs of linyphiids were commonly found attached to the pitcher rim, these spiders may have encountered the nectar more often than other groups.

Comparisons of spider assemblages at genus and species levels among capture techniques were all non-significant. This is likely due to the lack of statistical power. Unless mature, many spiders are not able to be identified to genus or species using conventional techniques because the identification of many groups requires fully developed genitalia (Ubick et al. 2017). Therefore, although we captured 1622 spiders that were able to be identified to family, only 739 were identified to genus (46% of the spiders identified to family) and only 516 to species (32% of the spiders identified to family). This drastic reduction in sample size likely caused non-significant results.

In contrast to the non-significant differences found at lower taxonomic levels, when organized by guild (which grouped families, so could therefore be thought of as at a higher taxonomic level than family), spider assemblages were significantly different among capture techniques. In fact, in post hoc tests, every comparison between each pair of assemblages was significantly different. While some rates of guild capture were similar between what was captured by the plant (CC) vs. what was found residing on the plant (RES; e.g., ambushers, ground runners), there were several marked differences (e.g., stalkers, sheet web-builders, and space web-builders; Table 3). An even greater contrast can be seen when comparing CC vs. what was captured by sweep net (SN + SB). However, these differences were less noticeable at the guild level when comparing CC vs. what was captured through PT (Table 3). Similarly, when organized by guild, those spider assemblages in the environment (SN + SB + PT) were significantly different from either RES or CC. Because guilds are amalgamations of similar families grouped by behavior, most of the differences among guild-based assemblages likely relate back to the family-linked behaviors mentioned previously (e.g., linyphiids building webs inside pitchers).

There was no significant difference in the Shannon–Wiener diversity of the spiders found among the different capture techniques when analyzed at higher taxonomic levels (family and genus). The lack of significance at higher taxonomic levels is likely a statistical artifact; as the number of categories into which specimens may be placed (fewer categories as taxonomic level increases), the probability of two locations having significant different diversity values decreases. However, when analyzed by species, SN + SB was significantly less diverse than PT. This difference is likely due to pitfall traps commonly capturing higher spider species richness than sweep nets (Churchill and Arthur 1999, Standen 2000).

Several pieces of evidence suggest that spider capture by *S. purpurea* is not random and that certain families are more likely to be captured than others. If the pitchers of *S. purpurea* acted like simple pitfall traps that captured spiders at random, then CC should have been very similar to PT, but it was not. In fact, the spider assemblage captured by *S. purpurea* (CC) was highly specific (clumping of CC in Fig. 1). Moreover, this specificity was maintained even across the hundreds of kilometers among locations and through the variety of

habitat differences that were present among the sites (e.g., pine barren vs. pond edge).

The abundance of spider families caught through CC was most similar to the abundance of spider families found near the plant as residents (RES; Fig. 1). This may be because many visits to pitchers by spiders are fatal. Therefore, our prey sampling near the plant (RES) may represent spiders most likely to visit the plant and therefore most likely to be captured. This high similarity between RES and CC spider prey composition, although statistically different, also suggests that spider residents—those building webs over, in, and on the plant—often become victims of the plant itself.

The rate of residency (RES) of spiders was not always tied to the abundance of the spider family within the environment (Table 2). This disparity may be, in part, due to our sampling method; transient ground spiders may have been less likely to be found than a sedentary web-residing spider within the short time the plants were sampled. In contrast, funnel-weaving spiders (Agelenidae) were much more common as residents than found in the environment, probably because agelenids often seek out vegetation to build their funnel webs (Foelix 2010), *S. purpurea* pitchers are often used as web locations (Milne 2012), and the spiders were sedentary and easier to find on the plant. Agelenids rarely were found as victims in pitchers, however. Moreover, agelenid webs commonly covered multiple *S. purpurea* pitchers, therefore possibly acting as direct competitors of arthropod prey. Spiders do compete with carnivorous sundews for prey (Jennings et al. 2010), but it is unknown if funnel-weaving spiders also act as competitors but with pitcher plants.

Because many *S. purpurea* populations are isolated relicts from a previously widespread population, genetic variability within individual populations is reduced, hypothetically due to genetic drift from isolation and reduced population size (Schwaegerle and Schaal 1979). Furthermore, separate isolated populations show increased genetic divergence (Taggart et al. 1990, Godt and Hamrick 1998, Parisod et al. 2004). Although there has been a good deal of study on how morphological features affect prey capture in *S. purpurea* (Cresswell 1993, Green and Horner 2007, Bennett and Ellison 2009), there has been less done on how genetic variability affects this variable. Because the genetic relationships among the pitcher plants were not measured in this study, it is unknown how genetic variability within each pitcher plant population affected these results.

These results suggest that *S. purpurea* is very selective in its spider capture regimen. Although the plant possesses a diet largely consisting of ants, spiders are its second-most common prey type (Ellison and Gotelli 2009). Foraging or building webs on pitchers and drinking nectar may render spiders vulnerable to becoming part of this diet. Employing tactics to evade capture and avoid drowning might increase their prospects of escape. Further research will be valuable in understanding how spiders navigate these options.

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Literature Cited

Amalin, D. M., J. E. Pena, J. Reiskind, and R. McSorley. 2001. Comparison of the survival of three species of sac spiders on natural and artificial diets. Journal of Arachnology 29:253–262.

Anderson, B., and J. J. Midgley. 2002. It takes two to tango but three is a tangle: mutualists and cheaters on the carnivorous plant *Roridula*. Oecologia 132:369–373.

Bennett, K. F., and A. M. Ellison. 2009. Nectar, not colour, may lure insects to their death. Biology Letters 5:469–472.

Churchill, T. B., and J. M. Arthur. 1999. Measuring spider richness: effects of different sampling methods and temporal scales. Journal of Insect Conservation 3:287–295.

Cipollini Jr., D. F., S. J. Newell, and A. J. Nastase. 1994. Total carbohydrates in nectar of *Sarracenia purpurea* L. (northern pitcher plant). American Midland Naturalist 131:374–377.

Cresswell, J. E. 1991. Capture rates and composition of insect prey of the pitcher plant *Sarracenia purpurea*. American Midland Naturalist 125:1–9.

Cresswell, J. E. 1993. The morphological correlates of prey capture and resource parasitism in pitchers of the carnivorous plant, *Sarracenia purpurea*. American Midland Naturalist 129:35–41.

Deppe, J. L., W. J. Dress, A. J. Nastase, S. J. Newell, and C. S. Luciano. 2000. Diel variation of sugar amount in nectar from pitchers of *Sarracenia purpurea* L. with and without insect visitors. American Midland Naturalist 144:123–132.

Ellison, A. M., and N. J. Gotelli. 2009. Energetics and the evolution of carnivorous plants – Darwin's 'most wonderful plants in the world'. Journal of Experimental Botany 60:19–42.

Fish, D., and D. W. Hall. 1978. Succession and stratification of aquatic insects inhabiting the leaves of the insectivorous pitcher plant, *Sarracenia purpurea*. American Midland Naturalist 99:172–183.

Foelix, R. F. 2010. Biology of spiders. Oxford University Press, New York, New York, USA.

Frost, C., and L. Musselman. 1987. History and vegetation of the Blackwater Ecologic Preserve. Castanea 52:16–46.

Godt, M. J., and J. L. Hamrick. 1998. Genetic divergence among intraspecific taxa of *Sarracenia purpurea*. Systematic Botany 23:427–438.

Green, M. L., and J. D. Horner. 2007. The relationship between prey capture and characteristics of the carnivorous pitcher plant, *Sarracenia alata* Wood. American Midland Naturalist 158:424–431.

Harwood, J. D., K. D. Sunderland, and W. O. C. Symondson. 2001. Living where the food is: web location by Linyphiid spiders in relation to prey availability in winter wheat. Journal of Applied Ecology 38:88–99.

Harwood, J. D., K. D. Sunderland, and W. O. C. Symondson. 2003. Web-location by Linyphiid spiders: prey-specific aggregation and foraging strategies. Journal of Animal Ecology 72:745–756.

Heard, S. B. 1998. Capture rates of invertebrate prey by the pitcher plant, *Sarracenia purpurea* L. American Midland Naturalist 139:79–89.

Jackson, R. R., S. D. Pollard, X. J. Nelson, G. B. Edwards, and A. T. Barrion. 2001. Jumping spiders (Araneae: Salticidae) that feed on nectar. Journal of the Zoological Society of London 255:25–29.

Jennings, D. T., B. Cutler, and B. Connery. 2008. Spiders (Arachnida: Araneae) associated with seed heads of *Sarracenia purpurea* (Sarraceniaceae) at Acadia National Park, Maine. Northeastern Naturalist 15:523–540.

Jennings, D. T., J. J. Krupa, T. R. Raffel, and J. R. Rohr. 2010. Evidence for competition between carnivorous plants and spiders. Proceedings of the Royal Society B: Biological Sciences. https://doi.org/10.1098/rspb.2010.0465

Jones, F. M. 1935. Pitcher plants and their insect associates. Pages 25–30 *in* M. V. Walcott, editor. Illustrations of North American pitcher plants. Smithsonian Institution, Washington, D.C., USA.

Judd, W. W. 1959. Studies of the Byron bog in Southwestern Ontario X. Inquilines and victims of the pitcher-plant, *Sarracenia purpurea* L. Canadian Entomologist 91:171–180.

Juniper, B. E., R. J. Robins, and D. M. Joel. 1989. The carnivorous plants. Academic Press, London, UK.

Lloyd, F. E. 1942. The carnivorous plants. The Ronald Press Company, New York, New York, USA.

Martinez, A. P. 2017. pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.0.1. https://github.com/pmartinezarbizu/pairwiseAdonis

McAlister, W. H. 1960. The diving and surface-walking behavior of *Dolomedes triton sexpunctatus* (Araneidae: Pisauridae). Animal Behavior 8:109–111.

Milne, M. A. 2012. The purple pitcher plant as a spider oviposition site. Southeastern Naturalist 11:567–574.

Milne, M. A., and D. A. Waller. 2013. Does pitcher plant morphology affect spider residency? Northeastern Naturalist 20:419–429.

Nahas, L., M. O. Gonzaga, and K. Del-Claro. 2016. Wandering and web spiders feeding on the nectar from extrafloral nectaries in neotropical savanna. Journal of Zoology 301:125–132.

Nyffeler, M., E. J. Olson, and W. O. C. Symondson. 2016. Plant-eating by spiders. Journal of Arachnology 44:15–27.

Parisod, C., C. Trippi, and N. Galland. 2004. Genetic variability and founder effect in the pitcher plant *Sarracenia purpurea* (Sarraceniaceae) in populations introduced into Switzerland: from inbreeding to invasion. Annals of Botany 95:277–286.

Plachno, B. J. 2007. "Sweet but dangerous": nectaries in carnivorous plants. Acta Agrobotanica 60:31–37.

Pollard, S. D., M. W. Beck, and G. N. Dodson. 1995. Why do male crab spiders drink nectar? Animal Behaviour 49:1443–1448.

R Development Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org

Schaefer, H. M., and G. D. Ruxton. 2008. Fatal attraction: Carnivorous plants roll out the red carpet to lure insects. Biology Letters 4:153–155.

Schnell, D. E. 2002. Carnivorous plants of the United States and Canada. Timber Press, Portland, Oregon, USA.

Schwaegerle, K. E., and B. A. Schaal. 1979. Genetic variability and founder effect in the pitcher plant *Sarracenia purpurea* L. Evolution 33:1210–1218.

Shochat, E., W. L. Stefanov, M. E. A. Whitehouse, and S. H. Faeth. 2004. Urbanization and spider diversity: influences of human modification of habitat structure and productivity. Ecological Applications 14:268–280.

Standen, V. 2000. The adequacy of collecting techniques for estimating species richness of grassland invertebrates. Journal of Applied Ecology 37:884–893.

Sunderland, K. D., A. M. Fraser, and A. F. G. Dixon. 1986. Distribution of linyphiid spiders in relation to capture of prey in cereal fields. Pedobiologia 29:367–375.

Taggart, J. B., S. F. McNally, and P. M. Sharp. 1990. Genetic variability and differentiation among founder populations of the pitcher plant (*Sarracenia purpurea* L.) in Ireland. Heredity 64:177.

Taylor, R. M. 2004. Plant nectar contributes to the survival, activity, growth, and fecundity of the nectar-feeding wandering spider *Cheiracanthium inclusum* (Hentz) (Araneae: Miturgidae). Dissertation. The Ohio State University, Columbus, Ohio, USA.

Ubick, D., P. Paquin, P. E. Cushing, and N. Dupérré, editors. 2017. Spiders of North America: an identification manual. American Arachnological Society, Keene, New Hampshire, USA.

Uetz, G. W., J. Halaj, and A. B. Cady. 1999. Guild structure of spiders in major crops. Journal of Arachnology 27:270–280.

Whitmore, C., R. Slotow, T. E. Crouch, and A. S. Dippenaar-Schoeman. 2002. Diversity of spiders (Araneae) in a savanna reserve, Northern Province, South Africa. Journal of Arachnology 30: 344–356.

Williams, S. E. 1976. Comparative sensory physiology of the Droseraceae: the evolution of a plant sensory system. Proceedings of the American Philosophical Society 120:187–204.

Wolfe, L. M. 1981. Feeding behavior of a plant: differential prey capture in old and new leaves of the pitcher plant (*Sarracenia purpurea*). American Midland Naturalist 106:352–359.

Wray, D. L., and C. S. Brimley. 1943. The insect inquilines and victims of pitcher plants in North Carolina. Annals of the Entomological Society of America 36:128–137.

Zamora, R. 1995. The trapping success of a carnivorous plant, *Pinguicula vallisneriifolia*: the cumulative effects of availability, attraction, retention and robbery of prey. Oikos 73:309–322.

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