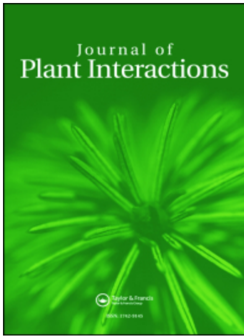

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Leaf litter capture in the carnivorous pitcher plant, *Sarracenia purpurea*: a preliminary study

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ABSTRACT
Diet breadth is a key life-history trait influencing range size, evolutionary trajectories, and ecosystem functioning. While diet breadth studies have traditionally been confined to animals, carnivorous plants provide an exciting conceptual extension to existing theory. We examine the possibility of diet breadth expansion in *Sarracenia purpurea*, a carnivorous pitcher plant, integrating field and greenhouse experiments with CHN analysis to quantify leaf litter consumption. Wild plants captured leaf detritus at levels comparable to insect prey. Pitchers fed leaf biomass in the field exhibited non-significant increases in foliar nitrogen, while the greenhouse experiment showed no effect of leaf litter. These results demonstrate that *S. purpurea* pitchers capture a substantial amount of leaf litter but show no clear evidence of nitrogen assimilation from this material. We found that short-term nitrogen acquisition from captured litterfall is minimal or absent in *S. purpurea* pitchers, especially relative to rapid nutrient assimilation from arthropod prey.

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Carnivorous plants; diet breadth; foliar nitrogen; leaf litter; pitcher plants; *Sarracenia purpurea*

Introduction

Dietary niche breadth has significant effects on ecosystem functioning and evolutionary processes (Forister et al. 2015). The extent of a species' resource specialization can determine its geographical range (Slatyer et al. 2013) and vulnerability to anthropogenic disruption and habitat fragmentation (Devictor et al. 2008). Diet breadth is also a critical predictor in trophic dynamics; predator specialization can regulate the relative importance of top-down and bottom-up control (Jiang and Morin 2005), and diet specialization by prey can even alter the severity of predation pressure in some systems (Dyer and Floyd 1993). Variation in diet breadth can also promote competitor coexistence within diverse communities (MacArthur 1958; Büchi and Vuilleumier 2014) and affect rates of coevolution and speciation (Janz et al. 2006; Schemske et al. 2009; Hardy et al. 2016). The study of species' diet breadth is thus critical in understanding its conservation, ecological interactions, and evolutionary history.

Carnivorous plants offer novel insights on dietary niche breadth; because they have evolved independently in multiple angiosperm lineages and use modified leaves to catch animal prey, comparing the leaf modifications among lineages can reveal convergent strategies for nutrient capture. Across the ~600 species of carnivorous plants in 12 families (Ellison and Gotelli 2001; Givnish 2015), pitfall traps have evolved independently at least six times (Givnish 2015) in genera including the well-studied North American *Sarracenia* and Southeast Asian *Nepenthes* pitcher plants. While the majority of pitcher plants capture and assimilate nutrients from arthropod prey, it is misleading to consider their traps strictly insectivorous. Morphological divergence is associated with a broad range of dietary specialization or expansion within some groups

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(Thorogood et al. 2017). Varying degrees of dietary specialization are especially apparent within *Nepenthes*, in which diverse pitcher morphology and geometry are often adaptations to different nutrient acquisition strategies (Gaume et al. 2016; Thorogood et al. 2017). Strategies range from trapping generalists, such as *N. gracilis,* which captures a broad range of insects (Moran et al. 1999), to refined specialists, such as *N. lowii*, which captures the fecal matter of mountain treeshrews, (Chin et al. 2010), and *N. albomarginata*, which specializes on termites (Moran et al. 2001). One distinct example of dietary expansion is *N. ampullaria*, a ground-dwelling detritivore that digests leaf litter in addition to arthropod prey (Moran et al. 2003; Pavlovič et al. 2011).

Like in *Nepenthes*, morphological variation between *Sarracenia* species may suggest variation in diet breadth. The well-studied *Sarracenia purpurea* has notable differences from its congeners and shares several traits with the unrelated *N. ampullaria*, whose particular morphology facilitates the capture and digestion of leaf detritus (Moran et al. 2003; Pavlovič et al. 2011). Firstly, *S. purpurea* is shorter and more cylindrical than many species in the genus (Bittleston et al. 2018), and has low prey capture efficiency, retaining less than one percent of visiting insects (Newell and Nastase 1998). Likewise, the pitchers of *N. ampullaria* are shorter than many congeners (Lam and Tan 2020), which has been predicted to reduce prey capture in other pitcher plant species (Green and Horner 2007; Bittleston et al. 2018; Sheridan et al. 2021). The pitchers of *S. purpurea* grow in dense clumps and each pitcher's 'lid' (operculum) is retracted from the pitcher mouth, allowing detritus to collect within the fluid (Figure 1) (Heard 1998; McPherson 2006). Additionally, this open orientation allows greater rainwater collection than in other *Sarracenia* species where the operculum position limits such accumulation (Heard 1994; Wakefield et al. 2005). *Nepenthes ampullaria* similarly grows in dense 'carpets' on the forest floor, and the plant's vestigial lid is also reflexed, enabling the capture of plant detritus (Moran et al. 2003; Pavlovič et al. 2011). Both species have limited production of key enzymes used in insect digestion (Adams and Smith 1977; Lam and Tan 2020), a trait linked to lower digestive efficiency in *N. ampullaria* (Gilbert et al. 2022). Instead, both host broad communities of symbiotic bacteria, protozoans, and insect larvae that act as specialized 'inquilines': digestive mutualists that live in the pitcher fluid and break down captured material, accelerating the release of soluble nutrients (Bradshaw and Creelman

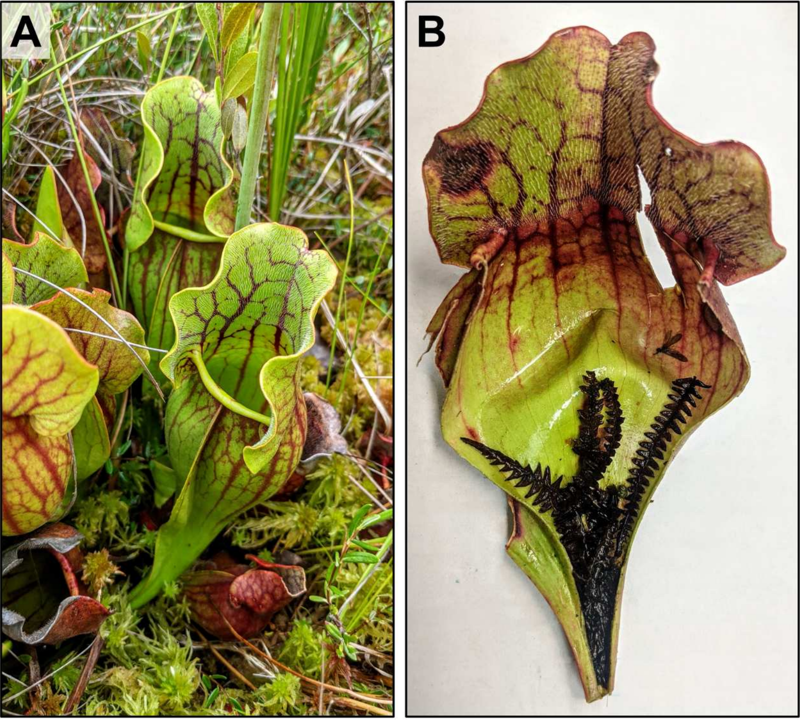

Figure 1. Pitcher morphology and leaf litter collection in *Sarracenia purpurea*. (a) A *Sarracenia purpurea* plant in situ with a retracted lid and exposed mouth, allowing leaf litter to fall in from above. (b) A dissected *S. purpurea* pitcher containing captured leaf biomass.

1984; Heard 1994; Mouquet et al. 2008; Moran et al. 2010; Luciano and Newell 2017). *S. purpurea* is nitrogen-limited (Ne'eman et al. 2006), and larvae of the mosquito *Wyeomyia smithii* and the midge *Metriocnemus knabi*—along with a community of bacteria and fungi—are known to mineralize organically bound nitrogen, making it available for pitcher uptake (Bradshaw and Creelman 1984; Mouquet et al. 2008; Adlassnig et al. 2011). For *N. ampullaria*, it is hypothesized that the rich inquiline community in the pitchers is important for leaf litter digestion (Moran et al. 2003, 2010) and that the relatively less acidic pitcher fluid may support this symbiotic assemblage (Moran et al. 2010). Similarly, *S. purpurea* has less acidic pitcher fluid than its congeners (Freund et al. 2022) and is known to sustain its own inquiline food web by oxygenating the pitcher fluid and maintaining homeostatic conditions (Bradshaw and Creelman 1984; Joel and Gepstein 1985; Sirota et al. 2013; Ellison et al. 2021). Cresswell (1998) found that over 50% of the biomass captured by *N. ampullaria* was leaf litter, and, using stable nitrogen isotope analysis, Moran et al. (2003) determined that around 35% of the plant's nitrogen was acquired through plant material. *S. purpurea* also accumulates substantial leaf litter (Heard 1998; McPherson 2006; Wheeler, personal observation), but the quantity and possible use of this resource was previously untested. While leaf litter consumption in *N. ampullaria* has been well studied, this mode of nutrient acquisition has not yet been studied in other pitcher plant lineages. *S. purpurea* shares many traits that are critical to *N. ampullaria's* detritivorous syndrome, raising the compelling possibility of leaf litter consumption and diet breadth expansion in this species.

We hypothesize that *Sarracenia purpurea* has a broader diet than just arthropod prey, also capturing and utilizing nitrogen from leaf detritus. To test this hypothesis, we conducted (1) a field survey in which we harvested wild pitchers, examined their prey contents, and measured their foliar nitrogen; (2) a longitudinal field survey in which we collected the prey contents from pitchers for 12 weeks to measure temporal variation in prey capture; (3) an in vitro field experiment in which we measured the ammonia released from leaf litter in model pitchers; and (4) in vivo field and greenhouse experiments in which we measured the foliar nitrogen of pitchers artificially fed leaf litter (Figure 2).

Materials and methods

Field site — From June to July 2022, we sampled a population of purple pitcher plants (*Sarracenia purpurea* L.) at Kellogg Biological Station's Brook Lodge (42.353377, −85.373378). The bog is a small sphagnum island with flora largely consisting of low-lying forbs and a few woody shrubs, including poison sumac (*Toxicodendron vernix* L.) and dogwood (*Cornus spp.* L.). The island supports approximately 50 mature *S. purpurea* plants. For the purposes of the study, an individual plant was considered a discrete rosette of pitchers or a cluster of tightly packed rosettes.

Quantifying mass of naturally captured leaf litter — To determine whether *S. purpurea* pitchers capture substantial amounts of leaf litter relative to insect matter, we collected the contents of one pitcher from each of 48 plants (Figure 2A). To examine leaf litter capture over the longest possible time interval we only selected old pitchers: those produced during the previous year. Leaf age was determined by red coloration, size, scarring, and leaf thickness. We removed pitcher fluid and contents in situ and harvested the entire pitcher leaf for CHN combustion analysis. In the lab, we dissected pitchers and flushed remaining contents using a pipette and deionized water (diH_2O). Pitchers were then placed in a drying oven at 70°C for 48 h to prepare them for CHN combustion analysis.

To quantify the captured plant biomass within the pitchers, we sorted pitcher contents into plant biomass and all other biomass (including inquilines) under a dissecting microscope. To be conservative in our designation of total plant biomass, any unidentifiable material was counted as non-plant biomass. Sorted biomass was dried and massed. Because foliar nitrogen concentration is used as a metric of nutrient assimilation and digestive efficacy in a range of carnivorous plant taxa (Schulze et al. 1997; Wakefield et al. 2005; Pavlovič et al. 2011), we measured foliar nitrogen of the wild-harvested leaves, grinding the dried pitcher tissue using a mortar and pestle, sieving the ground tissue, and analyzing it per the CHN combustion method of Robertson and VanderWulp (2019). In brief, tissue was packed into a foil tin and combusted in a Costech elemental combustion system (model ESC4010, Costech Analytical Technologies, Valencia, California, United States; see VanderWulp 2024 for model specific protocol), measuring total nitrogen content by detecting the gases produced during combustion.

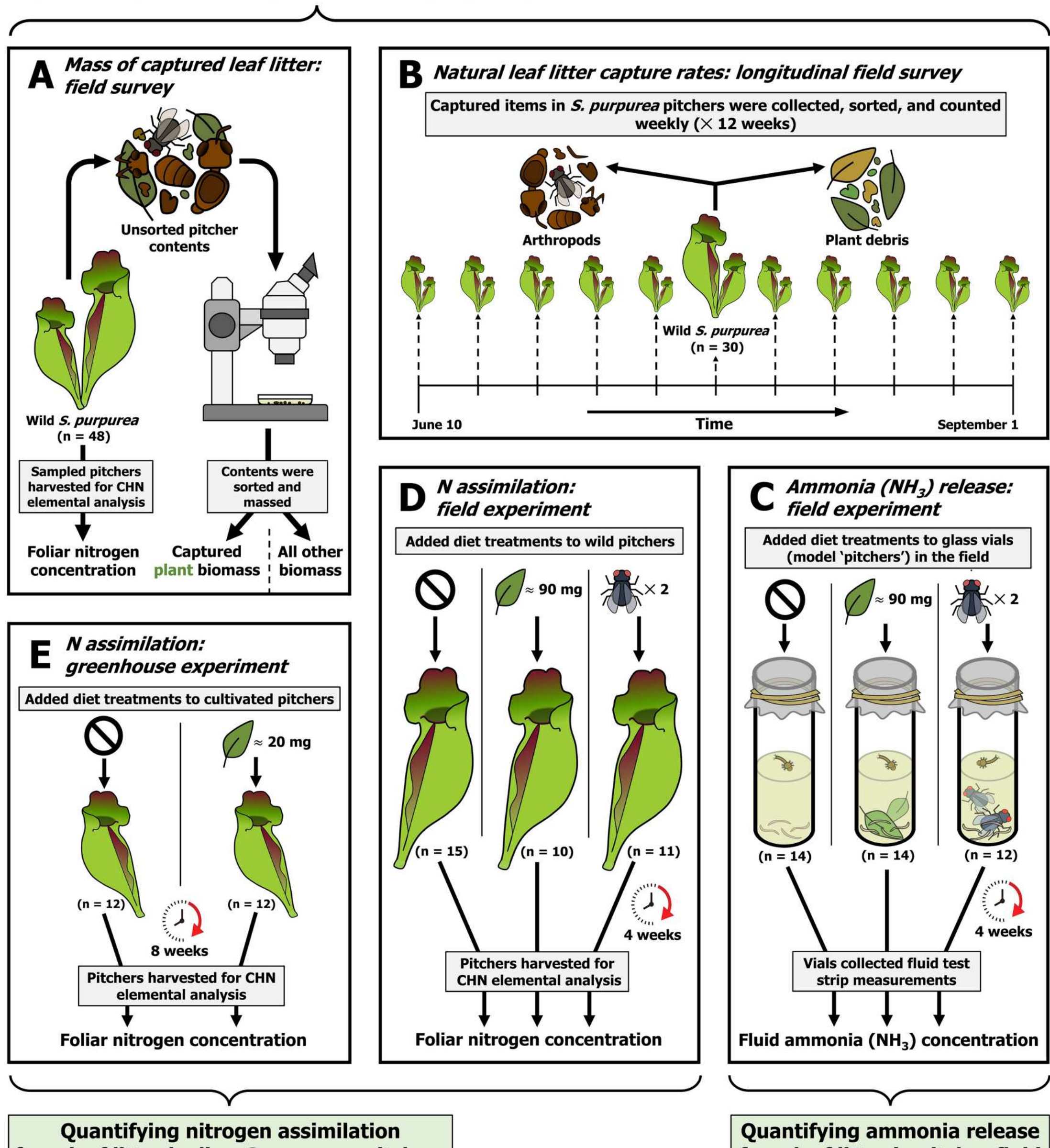

Figure 2. Experimental design overview for investigating leaf litter capture and nitrogen assimilation in *S. purpurea*. (A) Field survey quantifying captured leaf mass in wild pitchers (n = 48), with pitcher contents sorted under a microscope and foliar nitrogen of sampled pitchers measured by CHN combustion analysis. (B) Longitudinal field survey tracking the temporal variation in prey capture by a cohort of pitchers (n = 30) over 12 weeks, with pitcher contents sorted into plant debris items and arthropods and counted weekly. (C) In vitro ammonia release experiment, using artificial pitchers to measure NH_3 accumulation over four weeks from the digestion of three diet treatments (control, leaf litter, insect prey). (D) In vivo field experiment testing nitrogen assimilation from the same three treatments in live pitchers, with foliar nitrogen concentration measured after 4 weeks. (E) Greenhouse experiment on potted *S. purpurea* plants, measuring the effect of two diet treatments (control, leaf litter) on foliar nitrogen concentration to compare with the results of the field experiment under controlled conditions.

Quantifying leaf litter capture rate — To examine temporal variation in prey intake – including leaf litter – we conducted a longitudinal survey, collecting the entire prey contents from one pitcher per plant (n = 30) each week for 12 weeks from June 10 through September 1, 2022 (Figure 2B). Pitchers were emptied with a pipette and forceps, and contents including leaves, sticks, flower petals, seeds, and arthropods in each pitcher were identified and counted in the field. To minimize disruption to future prey capture, we refilled pitchers with distilled water after sampling.

Quantifying nitrogen release and accumulation in vitro — To compare the release of assimilable nitrogen from either leaf litter or insect prey sources into the pitcher fluid in the absence of absorption by the plant, we used glass vials approximately the size of natural pitchers (50 mL, 30 × 100 mm) to serve as model pitcher leaves for digestion experiments (Figure 2C). It has been well established that *S. purpurea* pitchers readily absorb inorganic nitrogenous compounds, especially ammonia, released from captured prey (Higley 1885; Hepburn et al. 1920; Bradshaw and Creelman 1984), so glass models were used instead of live pitchers to examine nitrogen release from diet treatments.

To set up these model pitchers, we first collected pitcher fluid and the two key macroinvertebrate inquilines – larvae of the midge *Metriocnemus knabi* and mosquito *Wyeomyia smithii* – from live *S. purpurea* pitchers in situ using plastic transfer pipettes. These two species only breed within *S. purpurea* pitchers and play an important role in digestion (Heard 1994). In the lab, we separated inquilines from the pitcher fluid, placing them in reverse osmosis (RO) water. We then homogenized the pitcher fluid by pouring it through a fine mesh, removing debris.

To create the model pitchers, we filled 40 glass vials with 20 mL of pitcher fluid and 15 mL of RO water. Each vial contained 35 mL of fluid, 4 midge larvae, 1 mosquito larva, and one of three diet treatments: control (n = 14), insect (n = 12), and plant (n = 14). The control treatment contained no food. The insect treatment consisted of two adult blue bottle flies (*Calliphora vicina*) sourced as pupae (USMantis Suppliers, Somers, New York, United States) and frozen once fully emerged. The approximate dry mass of two flies was 13.54 mg, and CHN combustion revealed that this treatment was equivalent to 1.49 mg of nitrogen input. To match the range of captured leaf litter we observed in wild pitchers, the plant treatment consisted of 90 mg leaf biomass, oven-dried at 70°C for 48 h and was a 1:1:1 mix of three common bog species: leatherleaf (*Chamaedaphne calyculata*, sourced from West Lake Bog, 42.188787, −85.582054), swamp loosestrife (*Decodon verticillatus*, sourced from the Brook Lodge field site), and marsh fern (*Thelypteris palustris var. pubescens*, sourced from the Brook Lodge field site). The 90 mg of leaf litter was equivalent to approximately 1.88 mg of nitrogen input. To prevent additional inquiline oviposition or accidental prey capture, we covered each tube with 4 layers of mesh (2 mm pore size). In mid-June 2022, we placed the glass tubes in the field alongside live *S. purpurea* plants and recovered them after 4 weeks. To test for the release of assimilable nitrogen from each diet treatment, we measured ammonia (NH_3) levels in the fluid using 0–6.0 mg/L Ammonia Test Strips (Hach, Loveland, Colorado, United States).

Quantifying nitrogen assimilation in vivo: field experiment — To measure assimilation of nitrogen from captured leaf litter in live *S. purpurea*, we conducted diet experiments under both field and greenhouse conditions. In the field, we added the same feeding treatments used in the in vitro experiment to live pitchers growing at the bog site (Figure 2D). One newly opened pitcher was chosen from each of 48 *S. purpurea* plants; young leaves were discerned by their green coloration, smaller size, leaf thinness, and absence of leaf scarring. Young pitchers were chosen for treatment application because pitchers are thought to be most active in their first year (Fish and Hall 1978). We emptied pitchers with a wide-bore plastic pipette, flushing the pipette several times to draw out all contents. To each pitcher, we added 4 midge larvae, 1 mosquito larva, and 1 of the three diet treatments described above: control, insect, or plant (n = 48 pitchers, 16 replicates per treatment). We poured these contents into the pitchers in mid-June, filling each pitcher to about two-thirds of its maximum capacity with RO water. To avoid additional prey or inquiline entry during the study period, each pitcher was covered entirely within a mesh drawstring bag (0.5 mm pore size).

After two weeks, we refilled the pitchers to two-thirds of their total volume with RO water if they were low or empty. After 4 weeks, we recovered pitchers for analysis of foliar nitrogen in the lab. We did not measure the ammonia concentration in the fluid of these pitchers, as they readily absorb the inorganic nitrogenous compounds that are present (Higley 1885; Hepburn et al. 1920; Bradshaw and Creelman 1984). We excluded pitchers that experienced repeated loss of fluid (generally drained from falling over or herbivore damage) or contained large prey that had managed to crawl under the mesh bag. This reduced our total sample to 36 replicates (control = 15, insect = 10, and plant = 11). We removed pitcher fluid and contents in situ and harvested the entire fed pitcher leaf for CHN combustion analysis. We chose to evaluate foliar nitrogen in the treated pitchers because young pitchers retain much of the nitrogen that they assimilate, and translocation to other plant tissues is gradual (Butler and Ellison 2007). In the lab, we dissected pitchers and flushed remaining contents using a pipette and RO water. Pitchers were placed in a drying oven at 70°C for 48 h. As with the mature leaves harvested to quantify natural leaf litter capture, foliar N was

measured from dried, ground, and sieved pitchers using a CHN elemental analyzer (described in '*Quantifying mass of naturally captured leaf litter*') per Robertson and VanderWulp (2019).

Quantifying nitrogen assimilation in vivo: greenhouse experiment — To supplement our findings from wild pitchers in field conditions, we conducted a complementary leaf litter addition experiment on *S. purpurea* plants grown in a greenhouse at the Kellogg Biological Station (Figure 2E). We purchased 24 mature *S. purpurea* plants (The Killer Plant Company, Fenton, Michigan, United States) and grew them in the greenhouse inside a mesh cage for several months before the start of the experiment to reduce nutrient differences between plants by uniformly excluding prey capture. We potted the plants in layered substrate, with the lower half of each pot containing a mix of peat and sand, and the upper half containing sphagnum moss. Temperature in the greenhouse was set not to exceed 20.5 °C at night and 21.6 °C in the day, and plants were tray-watered and grown under natural light conditions.

We conducted two rounds of diet additions on these plants, first May–July, then July–September 2023. Each round lasted 8 weeks. Both rounds were conducted on the same 24 plants, which were assigned one of two diet treatments: control (n = 12) and leaf litter (n = 12). The control treatment contained no food, and the leaf litter treatment contained 20 mg of dry foliar tissue of swamp loosestrife (*Decodon verticillatus*, sourced from Brook Lodge). The mass of the leaf litter treatment was chosen by scaling down the total mass of the treatment applied to the wild pitchers in the previous field experiment; these wild pitchers were larger than those in the greenhouse, so we reduced the previous 90 mg of leaf biomass to 20 mg based on the difference in average pitcher volume between the two groups. At the beginning of each round, we selected one large, fully open leaf per plant, filled it to two-thirds of its maximum capacity with RO water, and then added midge and mosquito larvae (collected from wild pitchers at the Brook Lodge field site) along with leaf litter, for those plants in the treatment group. To avoid additional capture during the experiment, each selected pitcher was individually covered with a mesh drawstring bag (0.5 mm pore size). Approximately 5 weeks after the start of each round, we replenished the inquiline populations in the pitchers, adding new mosquito and midge larvae (Appendix S1; see Supplemental Data with this article). After 8 weeks, the experimental pitchers from each round were harvested, flushed of contents, dried for 72 h at 70°C, and homogenized using TissueLyser II at 24 Hz for 5 mins with 2.38 mm metal beads (Qiagen).

Before drying the pitchers from each round, we dissected them and flushed all their remaining contents, following the same procedures described for the in vivo field experiment. We then dried, homogenized, and conducted CHN combustion analysis on harvested leaves to measure the foliar nitrogen concentration of each pitcher sample, also following the protocols described in previous sections.

In July 2025, we sampled and analyzed the nitrogen content of greenhouse potting media and bog soil to compare the nutritional content available to greenhouse and field plants through their roots. We collected five samples of each substrate type from the base of actively growing pitchers. The greenhouse plants were grown in a two-layer substrate, with peat/sand below and sphagnum moss above. To sample this substrate, we removed plants from their pots and collected equal amounts of sphagnum and peat/sand mix. To sample the bog soil, we collected material from near the base of pitcher plants distributed across the bog; each sample consisted of whatever mixed material was present directly adjacent to the plants, including roots, peat, sphagnum, and other organic material. These samples were then dried, homogenized, and analyzed for nitrogen content using CHN combustion analysis (described in '*Quantifying mass of naturally captured leaf litter*').

Statistical analysis — All statistical analyses were performed using R Statistical Software version 4.1.1 (R Core Team 2021). To test if captured leaf biomass predicted proportional foliar nitrogen content, we created a beta generalized linear mixed model (GLMM) using the package *glmmTMB* (Brooks et al. 2017), with plant biomass as the predictor of foliar nitrogen. To test for a relationship between pitcher diet treatment and foliar nitrogen from our in vivo experiments in the field and greenhouse, we used a beta GLMM (using *glmmTMB*), with treatment as the predictor and foliar nitrogen as the response. Experimental round was added as a random effect to the GLMM of foliar nitrogen from the greenhouse experiment. To assess the difference in soil nitrogen content between the bog and greenhouse, we created a beta GLMM with soil type as the predictor of soil nitrogen. A beta distribution was chosen for all nitrogen data because CHN analysis reports total nitrogen content as a proportion, and measured nitrogen values ranged from 0 to 1 (exclusive).

To test for a relationship between treatment and NH_3 in the in vitro study, we created a cumulative link model using the 'clm' function of the 'ordinal' package (Christensen 2022), treating the test strip ammonia values as ordered categories. Treatment type was used as the predictor in the in vitro ammonia model.

Results

Quantifying mass and capture rate of leaf litter — Of the 48 pitchers sampled for their preexisting contents, 81% contained some captured plant biomass. On average, there was 21 ± 30 mg (mean ± SD) of plant biomass within each pitcher, constituting 42 ± 32% of the total captured biomass per pitcher. Leaf litter comprised up to 90% of the contents by biomass in some pitchers. There was no significant correlation between plant biomass captured and foliar nitrogen concentration ($\beta = -0.798$, $Z = -0.85$, $p = 0.394$). Longitudinal sampling of prey items from June to September 2022 revealed that plant material was being captured by *S. purpurea* pitchers throughout the growing season, becoming most prominent in late summer. This increase in captured plant items was simultaneous with decreasing arthropod capture (Figure 3).

Quantifying nitrogen release and accumulation in vitro — In the in vitro digestion experiment, the NH_3 concentration in the insect-fed vials was significantly higher than that in control vials (Figure 4A, $\beta = 3.95$, $Z = 3.64$, $p < 0.001$). NH_3 concentration did not differ significantly between leaf-fed vials and control vials ($\beta = 1.24$, $Z = 1.36$, $p = 0.174$).

Quantifying nitrogen assimilation in vivo: field experiment — In the in vivo field experiment, the foliar nitrogen of insect-fed pitchers was significantly higher than that of control pitchers, showing a 0.89 standard deviation increase (Figure 4B, $\beta = 0.115$, $Z = 2.49$, $p = 0.0127$). We also observed an increase of 0.09% foliar nitrogen in leaf-fed pitchers relative to control pitchers (Figure 4B, $\beta = 0.0887$, $Z = 1.91$), representing a 0.68 standard deviation increase, but this difference was not significant ($p = 0.0562$).

Quantifying nitrogen assimilation in vivo: greenhouse experiment — In the in vivo greenhouse experiment, percent foliar nitrogen did not differ significantly between the leaf-fed and control pitchers (Figure 5, $\beta = -0.0138$, $Z = -0.190$ $p = 0.848$). Percent nitrogen was significantly different between bog and greenhouse soils, with greenhouse soil exhibiting lower nitrogen content than bog soils ($\beta = -0.643$, $Z = -7.96$, $p < 0.001$).

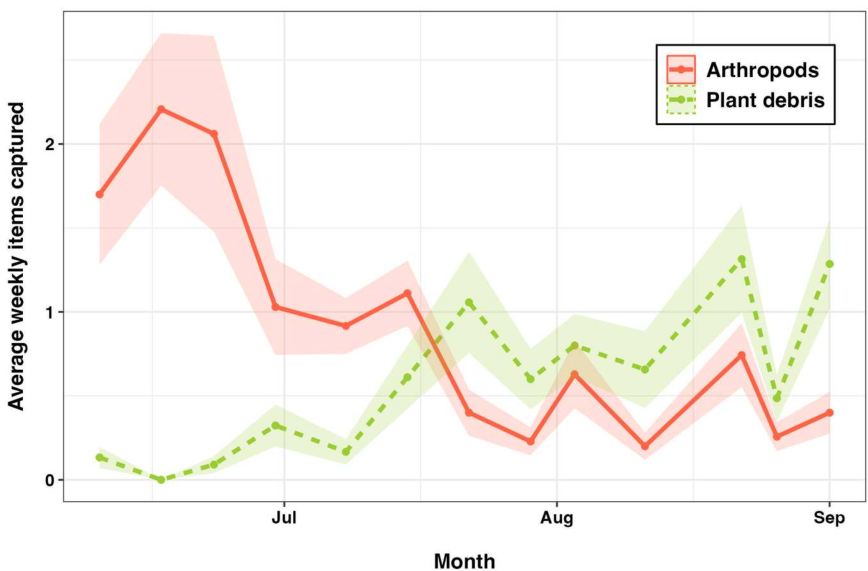

Figure 3. The average weekly count of captured plant items in wild *Sarracenia purpurea* pitchers (n = 30) increases in late summer, coinciding with a decrease in arthropod prey items. Captured plant items included leaves, sticks, flower petals, and seeds. Sampling was conducted over 12 weeks (June 10–September 1, 2022). Shaded regions indicate standard deviation.

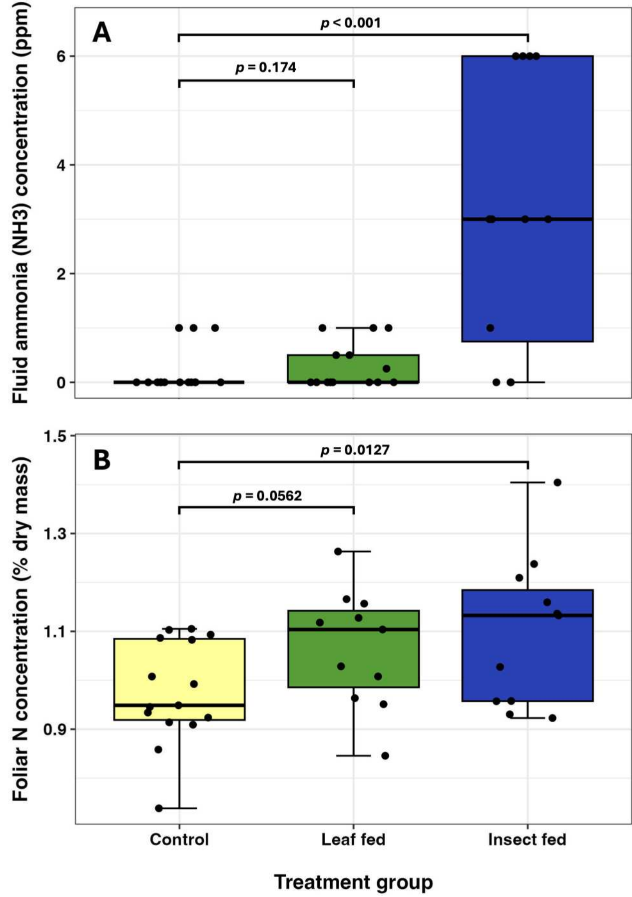

Figure 4. Results of the in vitro and in vivo diet addition experiments. (A) Ammonia (NH_3) concentration (parts per million) was significantly elevated in insect-fed vials relative to controls ($p < 0.001$), whereas the concentration in leaf-fed vials was not ($p = 0.174$). Ammonia was measured using 0–6.0 mg/L Ammonia Test Strips 28 days after administering the three separate diet treatments (control, n = 14; plant, n = 14; insect, n = 12). (B) In wild *Sarracenia purpurea* plants, foliar nitrogen concentration (percentage of the dry sample mass) was higher in insect-fed pitchers than in controls ($p = 0.0127$) Measured foliar nitrogen concentration was higher in leaf-fed pitchers than in controls, but this difference was not significant ($p = 0.0562$). Foliar nitrogen concentration was measured using CHN combustion analysis 28 days post-feeding (control, n = 15; plant, n = 11; insect, n = 10).

Discussion

We investigated the capture and assimilation of nitrogen from incidental leaf litter by the carnivorous plant *Sarracenia purpurea,* combining observational field surveys, manipulative field experiments (in vivo and in vitro), and combustion composition analysis. Leaf-litter utilization has been previously unassessed in this family of carnivorous pitcher plants. Our results do not provide support for the hypothesis that *S. purpurea* utilizes nitrogen from leaf litter – at least over the time frame in which plants are digesting insect prey – though we do confirm that the capture of leaf detritus is commonplace in this species. Despite convergent phenotypic similarities to the detritivorous *Nepenthes ampullaria* and comparably high observed litter-trapping, *S. purpurea* does not exhibit any clear short-term benefit from trapping litter.

Our study established that 81% of wild *S. purpurea* pitchers sampled contained leaf litter in situ and is the first to systematically quantify this phenomenon. Plant debris represented almost half of the average total biomass within each pitcher, a proportion similar to that found in the convergently-evolved pitcher plant *N. ampullaria*, which is known to digest leaf litter (Moran et al. 2003). We found no correlation between the mass of leaf litter naturally captured by a wild pitcher and its foliar nitrogen content, but this is unsurprising; after prey capture, *S. purpurea* pitchers gradually reallocate the nitrogen they sequester to the growth of new pitchers and other tissues (Butler and Ellison 2007). As a result, nitrogen assimilated from prey by an

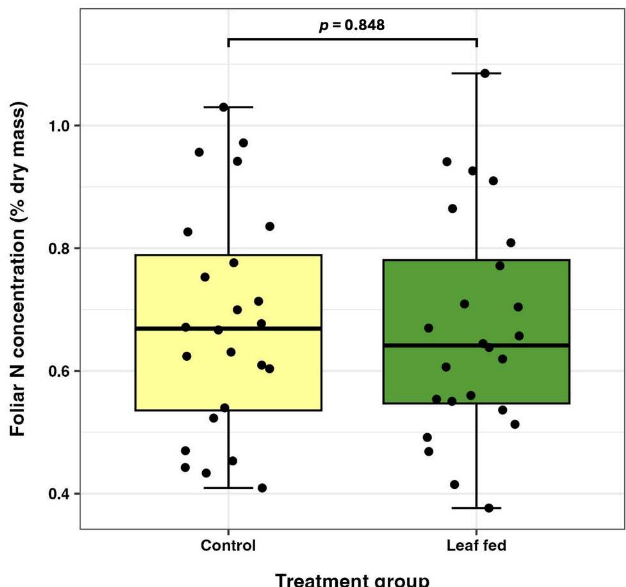

Figure 5. In *Sarracenia purpurea* plants grown in a greenhouse experiment, foliar nitrogen concentration (percentage of the dry sample mass) was not significantly different between leaf-fed and control pitchers ($p = 0.848$). Foliar nitrogen concentration was measured using CHN combustion analysis 8 weeks post-feeding (n = 24 pitchers, 12 replicates per treatment).

individual pitcher may not accumulate in its tissues, making it difficult to detect a direct relationship between life-long biomass capture and foliar nitrogen at a single point in time. In considering any hypothetical benefit of leaf litter as a nutrient source, its potential value may be a factor of temporal patterns in leaf availability; our longitudinal study indicates that litterfall capture tends to increase as arthropod prey counts decline in the *S. purpurea* diet (Figure 3). One possibility is that this transition is due to the onset of seasonal arthropod dormancy and leaf abscission in surrounding bog plants. Despite having lower nitrogen and phosphorus content than arthropod tissues, leaf detritus remains a common catch for *S. purpurea* pitchers.

Despite its prevalence in the field, our in vitro field experiment did not indicate that leaf litter provides nitrogen to the pitcher plant by increasing ammonia (NH_3) in the pitcher fluid. In glass vials, the breakdown of insect prey significantly increased the ammonia in pitcher fluid after 4 weeks (Figure 4A), corroborating that insect capture and digestion quickly provides measurable inorganic nitrogen for pitcher uptake. This was not found for leaf litter in pitcher fluid; measured ammonia in vials containing leaf biomass was slightly higher than that in control vials after 4 weeks (Figure 4A), but this difference was minute and not significant.

Similarly, our in vivo field study did not provide evidence of significant nitrogen acquisition from leaf litter in *S. purpurea* (Figure 4B). The significant foliar nitrogen increase in wild, insect-fed pitchers at the bog site demonstrates that nutrient uptake from prey was occurring during the 4-week experiment. While the observed foliar nitrogen concentration in leaf-fed pitchers was higher than controls after these 4 weeks, this increase was not statistically significant ($p = 0.0562$). Our greenhouse experiment also showed no effect of leaf litter treatment after 8 weeks (Figure 5). The potting substrate used to grow *S. purpurea* plants in this experiment had significantly lower nitrogen content than the substrate at the bog site. This confirms that the lack of treatment effect in the greenhouse experiment was not due to elevated substrate nitrogen reducing the need for nutrient uptake through the pitchers. Together, the in vivo greenhouse and field experiments indicate that nitrogen assimilation from leaf litter is negligible, at least over the duration of these experiments.

Considered together, the integrative results of this study confirm that leaf litter capture by *S. purpurea* is widespread, but reveal no short-term nitrogen benefit. The large majority of pitchers accumulate substantial leaf litter (81% of pitchers, averaging 42% of total captured biomass) yet our experiments did not detect any significant increase in ammonia or foliar nitrogen from leaf litter addition to artificial and live pitchers. This indicates that nitrogen assimilation from leaf litter is absent or minimal under the conditions tested. The significant nitrogen increase observed in insect-fed pitchers affirms the effectiveness of nutrient uptake from arthropod capture and demonstrates that our methods were capable of detecting nitrogen release and absorption when it occurs over periods of weeks to months. Although the plant litter treatment

contained more nitrogen than the insect treatment (1.88 mg vs. 1.49 mg), insect prey seems to provide a more readily assimilable form of nitrogen to *S. purpurea*.

Although we did not detect significant nitrogen release from leaf litter, litter decomposition in pitcher systems likely does release nutrients at very low levels or over extended periods, as it does in other fluid systems (e.g. bromeliads, tree-hole phytotelmata, aquatic ecosystems; Wallace et al. 1997; Endres and Mercier 2001; Marcarelli et al. 2011; Farjalla et al. 2016; Benavides-Gordillo et al. 2019; Cereghetti et al. 2025). Multiple mechanisms could theoretically contribute to nitrogen release from leaf detritus in pitcher plants, including passive leaching (Gupta et al. 1996; Yanoviak 1999) or microbial and insect inquiline degradation (Carpenter 1982; Fish and Carpenter 1982; Walker et al. 1991; Heard 1994; Yanoviak 2001; Mouquet et al. 2008; Moran et al. 2010). Given the decomposition of plant litter is slow compared to insect prey (Moran et al. 2003, 2010; Pavlovič et al. 2011), requiring breakdown of the cellulose wall, short-term experiments may not capture subtle, cumulative nutrient benefits. Because *S. purpurea* leaves can overwinter and capture prey during two separate growing seasons (Heard 1998), this study represented only a small fraction of each pitcher's life. This brevity, considering the non-significant trend of increased tissue nitrogen in leaf-fed pitchers in the field, suggests that future studies examining longer time periods may help clarify whether extended exposure to leaf litter affects nitrogen dynamics. Future analyses examining stable nitrogen isotope ratios ($\delta^{15}N$) could also clarify whether *S. purpurea* pitchers derive any meaningful nutrition from litterfall (e.g. Moran et al. 2003), but the findings of this study suggests that the relative contribution of leaf litter, if any, is likely minute in the total nitrogen budget.

The high incidence of leaf litter capture in *S. purpurea*, despite the lack of clear nutritional benefits, prompts questions about the plant's functional morphology and the ecological impact of leaf litter in the pitcher phytotelm. Morphological similarities between *S. purpurea* and the detritivorous *N. ampullaria* may not represent convergence for detritivory, and there are several alternative explanations for litter capture beyond measurable short-term nutrient effects. First, *S. purpurea* may still assimilate limited nitrogen from leaf litter over longer timescales than measured here. Alternatively, morphological traits associated with litter capture may represent evolutionary precursors towards detritivory, though this remains speculative without direct evidence. Finally, these morphological traits could have been selected for other reasons entirely, with litterfall capture being an incidental by-product of pitcher architecture rather than an adaptive trait. For example, the open pitcher orientation that permits leaf litter capture also enables nitrogen deposition through rainwater collection; *S. purpurea* is known to absorb both inorganic and organic nitrogen from rainwater and atmospheric deposition (Chapin and Pastor 1995; Ellison and Gotelli 2002; Butler and Ellison 2007). If leaf litter capture represents a nonadaptive consequence of pitcher morphology, this further raises questions about what effects litter accumulation does have in this pitcher system. Leaf litter capture could be functionally neutral (sensu Heard 1994), having no effect on pitcher nutrition or inquiline community dynamics. However, there may be ecological costs to litter accumulation. We observed higher mortality of key inquiline species (*Metriocnemus knabi* and *Wyeomyia smithii*) in the artificial pitchers containing leaf litter, which suggests plant detritus might negatively affect the pitcher digestive community (Bradshaw and Creelman 1984). Additionally, excessive buildup of plant detritus could serve as a platform for the escape of drowning insects, impacting prey retention in a carnivorous plant with already low capture efficiency (Newell and Nastase 1998). Future experimental work could investigate the possible effects on prey capture and mutualism stability, helping resolve the unclear role of leaf litter prevalence in *S. purpurea* pitchers.

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Author contributions

DAW and SME made equal contributions to the paper. Original conception: DAW; data collection: DAW, SME, and KJG; data analyses: SME, DAW; writing (initial draft): DAW; writing (revisions/comments): SME, KJG. All authors agree to be accountable for all aspects of this work.

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Data availability statement

All data and scripts for reproducing the results of this publication are openly available on DRYAD: https://doi.org/10.5061/dryad.95x69p8tf.

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