OIKOS

Research article

Heterospecific-neighbor-mediated changes in density and size increase prey capture by a carnivorous plant

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Oikos
2025: e11309
doi: 10.1002/oik.11309
Subject Editor:
Antonino Cusumano
Editor-in-Chief: Pedro Peres-Neto
Accepted 15 April 2025

Prey capture by carnivorous plants is influenced by plant traits, environmental factors and interactions with animals. However, little is known about how interactions with heterospecific plant neighbors affect prey capture. Here, we examined how prey capture by the carnivorous plant pink sundew *Drosera capillaris* was influenced by its dominant flowering neighbor yellow hatpin *Syngonanthus flavidulus* via two mechanisms: 1) changes in the density and size of sundews and 2) changes in the surrounding prey resource availability resulting from the attraction of insects to the flowerheads of *S. flavidulus*. In a seasonal pond habitat, we surveyed *D. capillaris* density, rosette diameter and prey capture, along with insect communities, across habitat patches with varying *S. flavidulus* densities. We also experimentally removed *S. flavidulus* flowerheads to test the effect of neighboring flowers on prey availability. We found that *D. capillaris* density was negatively associated with *S. flavidulus* density. Moreover, the rosette diameter of *D. capillaris* decreased with increasing intraspecific density, resulting in high densities of smaller-sized sundew individuals in the habitat with few *S. flavidulus* and low densities of larger-sized sundew individuals in the habitat with abundant *S. flavidulus*. Such variation in *D. capillaris* density and size influenced its prey capture, with sundews (low densities but larger-sized) in the habitat with high *S. flavidulus* densities capturing more prey items per area. We found no differences in the insect abundance or composition among habitats with varying *S. flavidulus* densities. Furthermore, experimental removal of *S. flavidulus* flowerheads did not alter prey availability compared to the unmanipulated habitats, suggesting flowerhead attraction did not alter the local prey resource pool. Our study provides novel insights into the ecological mechanisms underlying prey capture in carnivorous plants, underlining how interactions with heterospecific neighbors can drive density- and size-dependent prey resource acquisition.

Keywords: carnivorous plants, competition, density-size relationships, *Drosera*, neighbor effects, prey capture

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Introduction

Carnivorous plants attract and digest animal prey to meet nutrient demands (Albert et al. 1992, Król et al. 2012, Givnish 2015). Prey-derived nutrients allow carnivorous plants to overcome nutrient limitation in the soil and boost their performance. For example, increased prey input is associated with increased foliar chlorophyll content and photosynthetic efficiency, in turn resulting in higher growth rates and aboveground biomass (Farnsworth and Ellison 2008, Pavlovič et al. 2014). Moreover, prey addition enhances reproduction by increasing flower numbers and seed production (Thum 1988, Zamora et al. 1998). Thus, the ability to capture prey is fundamental to the fitness of carnivorous plants.

Various factors can influence the prey capture ability of carnivorous plants. Plant traits, particularly the physical features of the traps, are key determinants of prey capture success (Mithöfer 2022). For example, the number and size of prey captured generally increase with trap size (Green and Horner 2007, Krueger et al. 2020). The density of the carnivorous plants also affects prey capture rates, which have been shown to decrease with conspecific density in threadleaf sundew *Drosera filiformis* (Gibson 1991a). High conspecific densities can increase intraspecific competition for insect resources, thereby reducing the total mass and number of prey captured per individual (Thum 1989, Lam et al. 2018).

Besides intraspecific interactions, interspecific interactions with carnivorous and non-carnivorous neighboring plants can also influence prey capture by carnivorous plants, both positively and negatively. For instance, the pitcher plant *Nepenthes gracilis* catches more shared prey items when growing closer to a heterospecific carnivorous neighbor *N. rafflesiana* (Lam et al. 2018). On the other hand, prey capture efficiency in the pitcher plant *Sarracenia alata* increases when the heterospecific non-carnivorous neighbors were experimentally trimmed (Brewer 2003). Moreover, neighboring plant communities can shape the growth, trap size, and density of carnivorous plants via competition for light and soil nutrients (Brewer 2003, 2019, Brewer et al. 2021). Shifts in neighbors throughout succession can also affect prey capture (Paniw et al. 2018). However, no study has directly examined how heterospecific-neighbor-mediated changes in trap size and density may influence prey capture performance.

The two-partner nature of prey capture processes involves not only plant traits but also prey availability. By altering prey insect communities in the habitats, heterospecific neighbors can have indirect effects on carnivorous plants. In plant–pollinator interactions, it has been shown that the flowers of neighboring plants can facilitate the pollination of focal plant species by attracting insect pollinators (Moeller 2004). Similarly, neighboring plants can potentially influence prey capture by modifying the abundance, size and taxonomic composition of insects in the surroundings. For example, the presence of neighboring plant flowers is associated with higher insect capture by sundew species *D. makinoi* and *D. toyoakensis* (Tagawa et al. 2018).

In this study, we examined how prey capture by pink sundew *D. capillaris* may be influenced by the sympatric heterospecific non-carnivorous neighbor yellow hatpin *Syngonanthus flavidulus* in a seasonal pond habitat. *S. flavidulus* is the dominant neighboring plant species in the habitat and flowers during the growing season of *D. capillaris*. Various floral visitors of *S. flavidulus* have been documented, including plasterer bees (Colletidae), sweat bees (Halictidae), and leafcutting bees (Megachilidae). We compared *D. capillaris* density, traits (size and leaf number), and prey capture as well as the insect communities in habitat patches of varying *S. flavidulus* densities. Specifically, we tested two non-mutually exclusive mechanisms by which the neighboring *S. flavidulus* may influence prey capture by *D. capillaris*. 1) *S. flavidulus* may affect prey capture by mediating the density and size of *D. capillaris*. We expected a tradeoff relationship between density and size, with less dense but larger-sized *D. capillaris* individuals capturing more prey items and vice versa (mechanism 1 in Fig. 1). 2) *S. flavidulus* may influence prey capture by changing the surrounding insect communities and thus prey availability. Specifically, the flowerheads of *S. flavidulus* may attract more insects to the surroundings, and we predicted higher prey capture by *D. capillaris* when *S. flavidulus* is more abundant (mechanism 2 in Fig. 1).

Material and methods

Study site and field sampling

The study was conducted in a seasonal pond habitat within a scrub flatwood landscape at Archbold Biological Station in Florida, USA (27°10′50″N, 81°21′00″W) (Fig. 2a). The station is atop the Lake Wales Ridge. This is the highest and oldest ridge in Florida and stretches nearly 160 kilometers along the center of the state. These ancient dunes were once islands when the bulk of Florida was underwater and represent some of the oldest habitats in the state. Today, the water level of seasonal ponds along the ridge varies throughout the year.

During the dry season (October to May), *D. capillaris* grows around the periphery of seasonal ponds in three apparent habitat patches with visually distinct densities of *S. flavidulus* (Fig. 2b). Within each habitat patch, *S. flavidulus* densities were fairly uniform. The outer patch (< 1 m from the pond edge) is characterized by exposed sand with sparse *S. flavidulus* (the 'low' *S. flavidulus* density habitat); the middle patch (1–2 m from the pond edge) is characterized by intermediate cover of *S. flavidulus* (the 'medium' *S. flavidulus* density habitat); the inner patch (> 2 m from the pond edge) is characterized by dense *S. flavidulus* (the 'high' *S. flavidulus* density habitat) (Fig. 2c–e). We selected ten 0.5 × 0.5 m plots in each habitat patch around a seasonal pond in April 2024. In each plot, we counted the number of *D. capillaris* individuals and *S. flavidulus* flowerheads, and collected 2–5 *D. capillaris* individuals for plant trait measurement and prey examination. A total of 41, 37 and 27 *D. capillaris* individuals were collected from the low, medium, and high *S. flavidulus* density habitats, respectively.

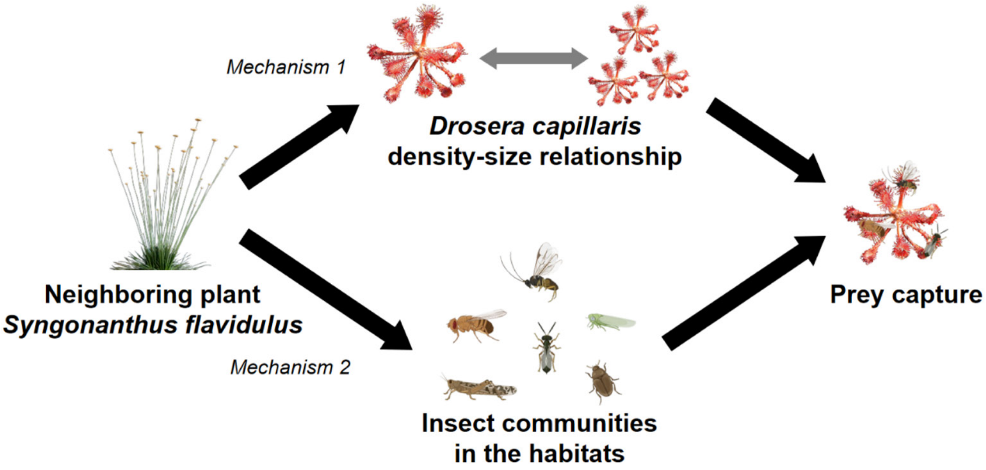

Figure 1. Two mechanisms by which the sympatric neighboring plant yellow hatpin *Syngonanthus flavidulus* may influence prey capture by pink sundew *Drosera capillaris*. In mechanism 1, *S. flavidulus* mediates the density and size of *D. capillaris* through a tradeoff relationship (less dense but larger-sized versus denser but smaller-sized). This influences prey capture by *D. capillaris* as prey capture is density- and trap-size-dependent. In mechanism 2, *S. flavidulus* alters the insect communities in the habitats, which in turn influences prey capture via changes in prey resource availability. Specifically, we hypothesize that the flowerheads of *S. flavidulus* may attract more insects to the surroundings, thereby increasing prey capture by *D. capillaris*.

Examination of sundew traits and prey capture

For each sampled *D. capillaris* individual, we measured the rosette diameter and the total number of leaves (both healthy leaves, which were bright red with mucilage at the tip of the glandular trichomes, and unhealthy leaves, which were pale red without mucilage at the tip of the trichomes). We recorded the total number of prey items and the taxonomic information of each prey on all the leaves. Because most prey items were partially digested, obfuscating detailed identification, we initially classified them into broad taxonomic groups (fly, wasp, hopper, etc.) and later into insect orders for further analysis. Non-insect prey items were classified as 'non-insect' and treated as an equivalent of insect order. Moreover, we were not able to accurately measure the prey size because of prey digestion, we therefore categorized the prey items into three size categories (small: < 1.5 mm; medium: 1.5–2.5 mm; large: > 2.5 mm) and assigned a size score to each category (small: 1; medium: 2, large: 3) as a proxy for the actual prey size.

Insect communities in the habitats

We sampled the insect communities in the three habitat patches of varying *S. flavidulus* densities by placing an 8 × 8 cm light yellow sticky fly trap (Supporting information) at the center of each plot on a sunny day (typical of the weather conditions during the dry season). This survey method provides useful information on the potential prey resource pool in the surroundings and has been used in studies on prey capture by sundew species (Jennings et al. 2010, Foot et al. 2014, Jürgens et al. 2015, Potts and Krupa 2016). The trap was placed horizontally and elevated above the ground level by 0.5–1 cm (the height of sundew leaves) for two days before being brought back to the lab for examination. To examine the effect of *S. flavidulus* flowerheads on the insect communities, we selected additional ten 0.5 × 0.5 m plots in the 'high' *S. flavidulus* density habitat and experimentally removed the flowerheads (the 'removal' plots; each removal plot was paired with a plot of high *S. flavidulus* density at a distance of 0.2–0.3 m to reduce the probability of trapping insects from the paired plot). The insect communities in these flowerhead removal plots were surveyed via sticky traps following the aforementioned procedure. To make the insect communities comparable to the captured prey items, we characterized the insects on the traps following the same procedure for the captured prey examination and assigned them to the aforementioned three size categories.

Data analyses

Plant densities and traits

To compare plant densities in the three habitat types, we fit generalized linear mixed effects models (GLMMs) with the number of *S. flavidulus* flowerheads and *D. capillaris* individuals in each plot as the responses, habitat type as the fixed effect, and plot as the random effect. We used a negative binomial error distribution with a log link function in both models to account for data overdispersion. The choice of a negative binomial distribution is particularly relevant for count data with variance exceeding the mean, which is common in ecological datasets. To examine the variation in sundew traits among habitat types, we fit (G)LMMs with *D. capillaris* rosette diameter and total leaf number as the responses, habitat type as the fixed effect, and plot as the random effect. For rosette diameter, we used a Gaussian error distribution because this response is continuous and normally distributed; for total leaf number, we used a Poisson error distribution with a log link function because there was no significant data overdispersion. We also examined the bivariate relationship between the density and rosette diameter of *D. capillaris* using a linear model.

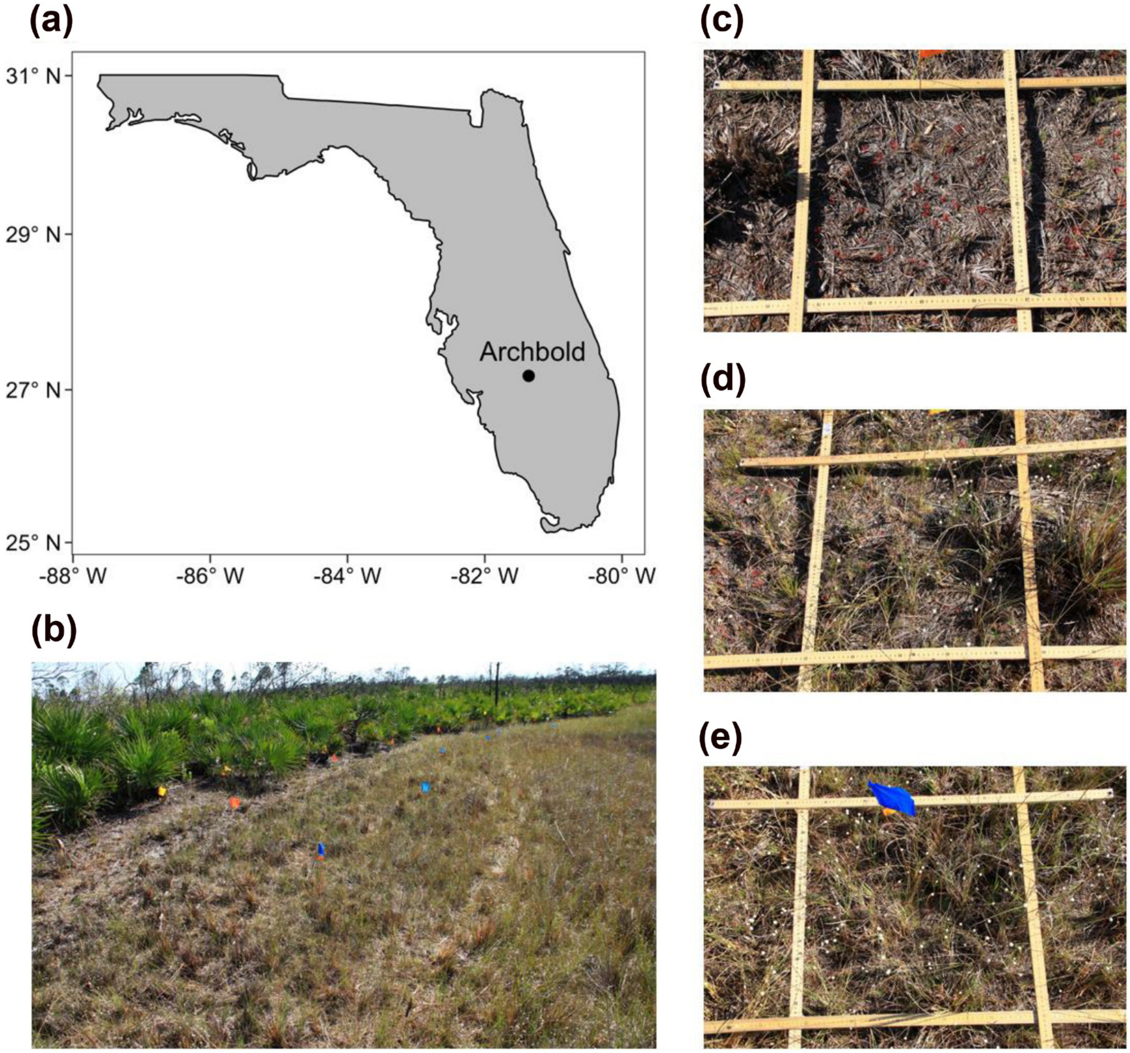

Figure 2. (a) A map of the study site, (b) a photo of the seasonal pond, and the sampling plots in the (c) 'low', (d) 'medium', and (e) 'high' neighbor *Syngonanthus flavidulus* density habitat.

Prey capture by sundew

To compare prey capture by *D. capillaris* in the three habitat types, we fit an LMM with the number of prey items captured per sundew area (cm^2, calculated as rosette diameter/2 $\times$ π) as the response, habitat type as the fixed effect, and plot as the random effect. Total leaf number was included as a covariate. Because prey items varied in their sizes, we also calculated prey-size-weighted capture by multiplying the number of prey items by their size scores to better represent the overall prey resource inputs. We compared prey-size-weighted capture per sundew area in the three habitat types using the LMM with the same model structure as the analysis of the number of prey items captured per sundew area. We also examined the bivariate relationships between the density/size of *D. capillaris* and prey capture (number of prey items captured per sundew area and prey-size-weighted capture per sundew area) using linear models.

To determine whether the taxonomic composition of the prey items captured by *D. capillaris* varied among the three habitat types, we performed permutational multivariate analysis of variance (PERMANOVA) on the prey order community matrix (number of prey items in each order captured by each sundew individual) based on Bray–Curtis dissimilarity using the *adonis2()* function (999 permutations) in the R 'vegan' package (Oksanen et al. 2022). Habitat type was included as the predictor. To test the assumption of homogeneity of multivariate dispersions in PERMANOVA, we performed permutational multivariate analysis of dispersion from group centroid (PERMDISP) using the *betadisper()* and *permutest()* function (999 permutations) in the R 'vegan' package. Prey taxonomic composition was visualized with non-metric multidimensional scaling (NMDS) ordination ($k = 3$ dimensions) based on Bray–Curtis dissimilarity. We also performed the same multivariate analysis on the prey size category community matrix (number of small, medium, and large prey items captured by each sundew individual) to assess the prey size (dis)similarity among habitat types.

Insect communities in the habitats

To better represent the potential prey resource pool for sundew, we excluded insect items that were larger than the largest prey item on the *D. capillaris* individuals examined (> 4 mm) for all following analyses of insect communities in the habitats. To compare insect abundance in the three unmanipulated habitats with varying *S. flavidulus* densities and the plots with *S. flavidulus* flowerheads removed, we fit a GLM with a negative binomial error distribution with the number of insect items on the sticky trap as the response and habitat type (including the 'removal' plots) as the fixed effect. We also calculated the insect-size-weighted number by multiplying the number of insect items by their size scores and compared the insect-size-weighted number among habitat types using the GLM with the same model structure as the analysis of the number of insect items.

To determine whether the taxonomic composition of insect communities varied among habitat types, we performed PERMANOVA on the insect order community matrix (number of insect items in each order on the sticky trap in each plot) based on Bray–Curtis dissimilarity using the *adonis2()* function (999 permutations) in the R 'vegan' package (Oksanen et al. 2022). Habitat type was included as the predictor. We also performed PERMDISP using the *betadisper()* and *permutest()* function (999 permutations) in the R 'vegan' package. Insect taxonomic composition was visualized with NMDS ordination ($k = 3$ dimensions) based on Bray–Curtis dissimilarity. We also performed the same multivariate analysis on the insect size category community matrix (number of small, medium, and large insect items on the sticky trap in each plot) to assess the insect size (dis)similarity among habitat types.

All GL(M)Ms were fitted via the *glmmtmb()* function in the R 'glmmTMB' package (Brooks et al. 2017). Model assumptions were checked via the simulated scaled residuals generated from the *simulateResiduals()* function in the R 'DHARMa' package (Hartig 2022). We assessed predictor significance using the Wald χ^2 test via the *Anova()* function (type II sums of squares) in the R 'car' package (Fox and Weisberg 2019). Pairwise comparisons between the estimated marginal means (EMMs) of treatment levels with the Tukey multiplicity adjustments were performed via the R 'emmeans' package (Lenth 2024). All analyses were performed in R ver. 4.3.3 (www.r-project.org).

Results

Plant densities and traits

The density of *S. flavidulus* flowerheads varied among habitat types ($\chi^2_2 = 282.7$, $p < 0.001$); the flowerhead density was the highest in the high *S. flavidulus* density habitat and the lowest in the low *S. flavidulus* density habitat (Fig. 3a). The density of *D. capillaris* also varied among habitat types ($\chi^2_2 = 320.7$, $p < 0.001$); however, *D. capillaris* density was the highest in the low *S. flavidulus* density habitat and the lowest in the high *S. flavidulus* density habitat (Fig. 3b). The size (rosette diameter) of *D. capillaris* varied among habitat types ($\chi^2_2 = 140.0$, $p < 0.001$) and was the largest in the high *S. flavidulus* density habitat (Fig. 3c). Total leaf number of *D. capillaris* was higher in the high *S. flavidulus* density habitat compared to the other two habitat types ($\chi^2_2 = 27.6$, $p < 0.001$, Fig. 3d). Across all three habitat types, *D. capillaris* size decreased with increasing intraspecific density ($\chi^2_1 = 102.3$, $p < 0.001$; Supporting information).

Prey capture by sundew

Both the number of prey items captured per sundew area and the prey-size-weighted capture per sundew area varied among habitat types (number of prey items: $\chi^2_2 = 38.6$, $p < 0.001$; prey-size-weighted capture: $\chi^2_2 = 31.3$, $p < 0.001$) and were higher in the high *S. flavidulus* density habitat compared to the other two habitat types (Fig. 4a–b). The number of prey items captured per sundew area decreased with *D. capillaris* density ($\chi^2_1 = 49.1$, $p < 0.001$, Fig. 4c) but increased with *D. capillaris* size ($\chi^2_1 = 53.4$, $p < 0.001$, Fig. 4d). Similarly, the prey-size-weighted capture per sundew area decreased with *D. capillaris* density ($\chi^2_1 = 45.1$, $p < 0.001$; Supporting information) but increased with *D. capillaris* size ($\chi^2_1 = 48.6$, $p < 0.001$; Supporting information).

The taxonomic composition of prey captured by *D. capillaris* varied among habitat types (PERMANOVA: $F_{2,100} = 31.7$, $p = 0.001$, $R^2 = 0.39$, Fig. 4e), with a considerable increase in the number of Diptera prey captured in the high (an average of 12.4 Diptera prey per *D. capillaris* individual) versus low (2.9 Diptera prey) and medium (3.8 Diptera prey) *S. flavidulus* density habitat (Supporting information). Furthermore, the result of PERMDISP was not significant ($F_{2,100} = 0.17$, $p = 0.87$), indicating that the assumption of homogeneity of multivariate dispersions in PERMANOVA was met. Similar results were found for the size composition of the prey captured (PERMANOVA: $F_{2,100} = 24.9$, $p = 0.001$, $R^2 = 0.33$; PERMDISP: $F_{2,100} = 2.3$, $p = 0.11$, Fig. 4f). Specifically, *D. capillaris* individuals captured more small- and medium-sized prey items in the high *S. flavidulus* density habitat (an average of 12.2 small- and 1.0 medium-sized prey per sundew) compared to the low (2.7 small- and 0.3 medium-sized prey) and medium (3.7 small- and 0.2 medium-sized prey) *S. flavidulus* density habitats (Supporting information).

Insect communities in the habitats

Both the number of insects on the sticky traps and the insect-size-weighted number did not vary significantly among the three unmanipulated habitats with varying *S. flavidulus* densities and the plots with *S. flavidulus* flowerheads removed (number of insects: $\chi^2_3 = 7.1$, $p = 0.07$; insect-size-weighted number: $\chi^2_3 = 7.7$, $p = 0.05$, Fig. 5a–b); the removal of *S. flavidulus* flowerheads did not affect the number of insects or the insect-size-weighted number compared to the high *S. flavidulus* density habitats (number of insects: EMM contrast = 1.5,

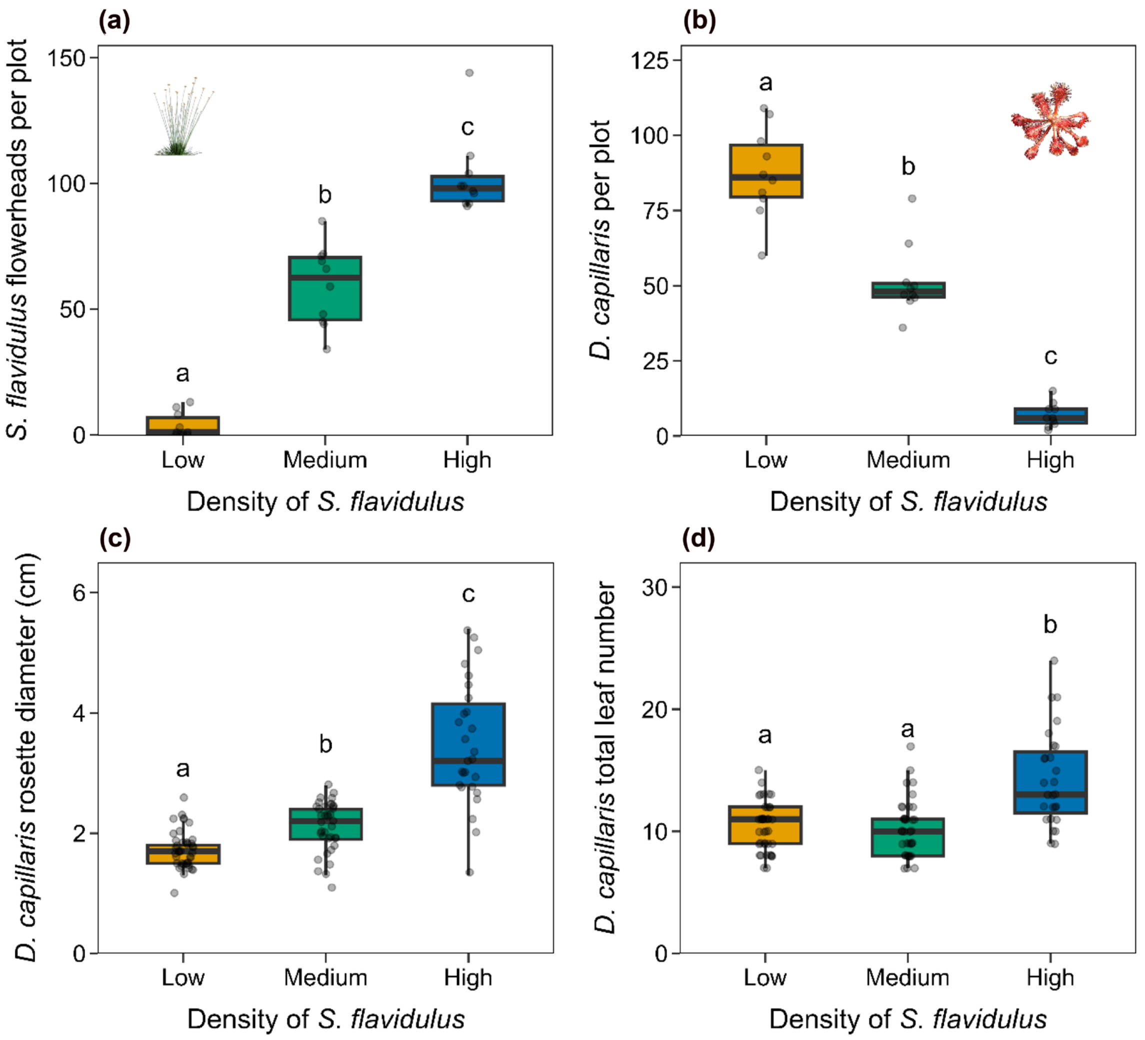

Figure 3. Plant densities and traits in the three habitat types of varying neighboring *S. flavidulus* densities. (a) Density (number per plot) of *S. flavidulus* flowerheads, (b) density (number per plot) of *D. capillaris,* (c) rosette diameter of *D. capillaris,* (d) total leaf number of *D. capillaris*. Points in (a) and (b) represent plots; points in (c) and (d) represent *D. capillaris* individuals. Letters denote significant differences with the Tukey multiplicity adjustment ($\alpha = 0.05$).

$Z = -0.9$, $p = 0.82$; insect-size-weighted number: EMM contrast = 1.5, $Z = -0.5$, $p = 0.96$).

Removal of *S. flavidulus* flowerheads did not significantly affect the taxonomic composition of insects on the sticky traps (PERMANOVA: $F_{3,36} = 1.7$, $p = 0.08$, $R^2 = 0.12$; PERMDISP: $F_{3,36} = 2.1$, $p = 0.12$, Fig. 5c, Supporting information). Likewise, the size composition of insects did not vary among the three unmanipulated habitats and the *S. flavidulus* flowerhead removal plots (PERMANOVA: $F_{3,36} = 0.4$, $p = 0.94$, $R^2 = 0.03$; PERMDISP: $F_{3,36} = 1.1$, $p = 0.37$, Fig. 5d, Supporting information).

Discussion

We explored two mechanisms by which plant neighborhood may influence prey capture by the carnivorous plant *D. capillaris* via 1) changes in density and size of *D. capillaris* and 2) changes in the insect prey communities in the surroundings. We found that prey capture by *D. capillaris* (number of prey items, prey-sized-weighted number, and prey taxonomic/size composition) varied among habitats with varying neighboring *S. flavidulus* densities. We also found that *D. capillaris* density was negatively associated with *S. flavidulus* density, and that *D. capillaris* size further decreased with *D. capillaris* density, resulting in more abundant but smaller sundew individuals in the habitat with low *S. flavidulus* densities and sparser but larger sundew individuals in the habitat with high *S. flavidulus* densities. Such variation in *D. capillaris* density and size was associated with variation in prey capture among habitat types, with more prey items captured per sundew area in the habitat with high densities of *S. flavidulus*. Interestingly, our sticky trap survey showed no major difference in the insect communities (number of insects, insect-size-weighted number and insect taxonomic/size composition) among the habitats with varying *S. flavidulus* densities. Moreover,

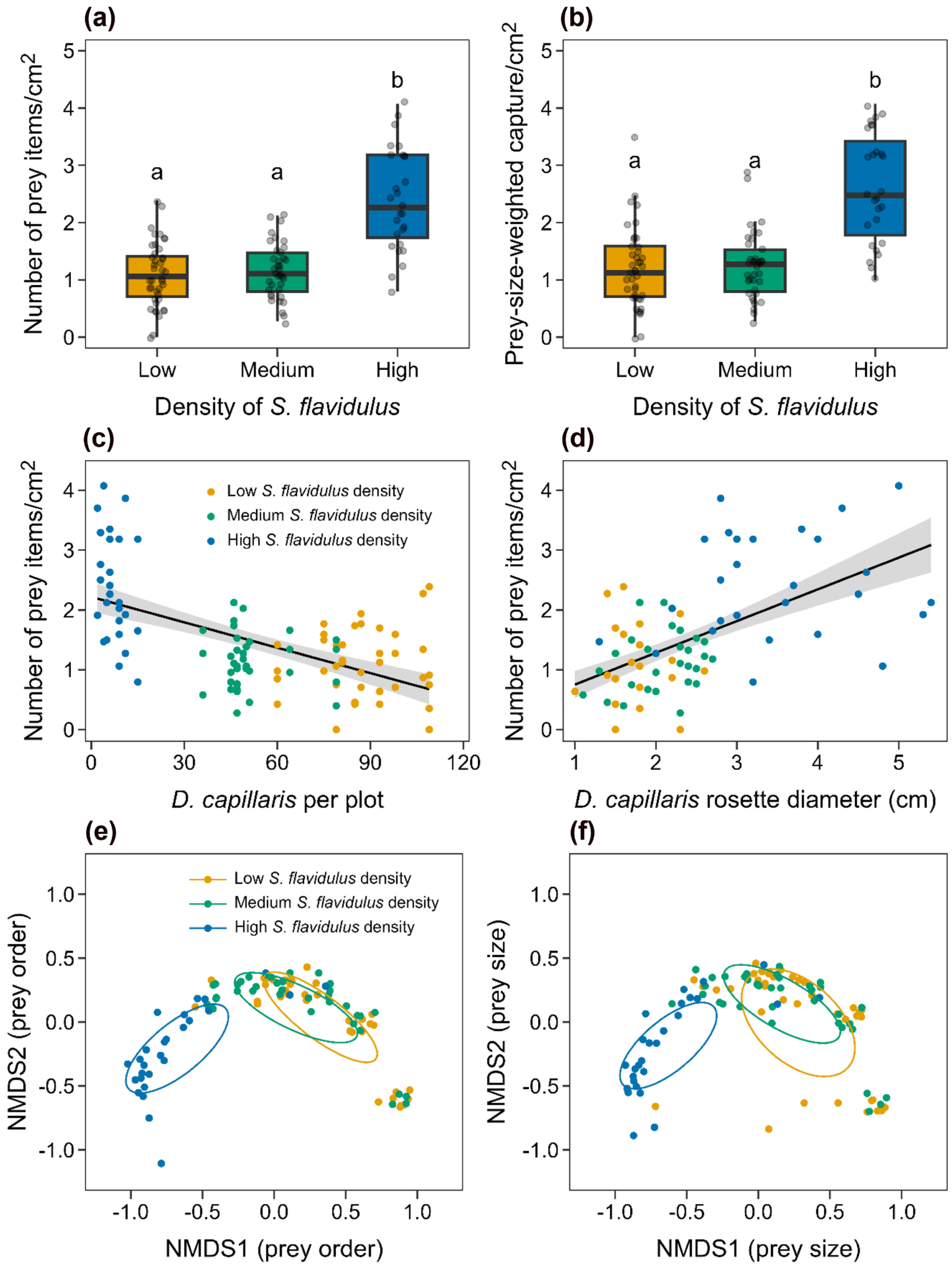

Figure 4. Prey capture by *D. capillaris* in the three habitat types of varying *S. flavidulus* densities. Points represent *D. capillaris* individuals. (a–b) Number of prey items captured per sundew area and prey-size-weighted capture per sundew area in the three habitats. Letters denote significant differences with the Tukey multiplicity adjustment ($\alpha = 0.05$). (c–d) The relationship between *D. capillaris* density/size (rosette diameter) and the number of prey items captured per sundew area across the three habitat types of varying *S. flavidulus* densities. Lines represent the relationships predicted from the models; shaded areas represent the 95% confidence intervals. (e–f) NMDS of the taxonomic (order) and size composition of prey captured by *D. capillaris* in the three habitats based on Bray–Curtis dissimilarity (stress = 0.02 and 0.03, respectively). Ovals represent the standard ellipse areas.

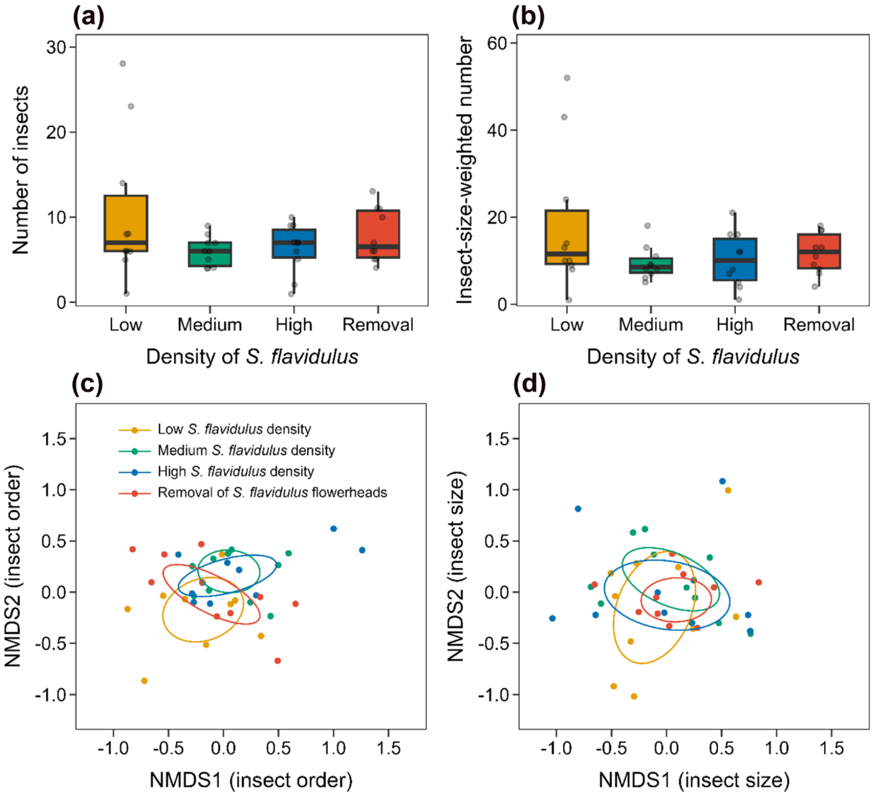

Figure 5. Insect communities in the three unmanipulated habitats with varying *S. flavidulus* densities and the plots with *S. flavidulus* flowerheads removed ('Removal'). Points represent the sticky trap samples in the plots. (a–b) Number of insects on the stick traps and insect-size-weighted number. (c–d) NMDS of the taxonomic (order) and size composition of insects on the sticky traps based on Bray–Curtis dissimilarity (stress = 0.07 and 0.08, respectively). Ovals represent the standard ellipse areas.

experimental removal of *S. flavidulus* flowerheads did not alter the insect communities compared to those in the unmanipulated habitats, suggesting little influence of *S. flavidulus* flowerheads on prey resource pool at the local scale. Taken together, these results indicate that heterospecific neighboring plants can influence prey capture by carnivorous plants via a density–size relationship (mechanism 1 in Fig. 1) – *S. flavidulus*-mediated variation in the density and size of *D. capillaris* is likely the main driver for its differential prey capture among the habitats in this system.

The dominant neighboring plant *S. flavidulus* had a strong negative impact on the density of *D. capillaris*, potentially due to interspecific competition for light and nutrients (Brewer 1998, Huang and Kao 2021). Consequently, *D. capillaris* density was higher in the habitats with lower *S. flavidulus* densities and vice versa. Moreover, the size of *D. capillaris* was negatively associated with its density – we observed the smallest sundew size in the habitat where *D. capillaris* was the most abundant (and the *S. flavidulus* density was the lowest) and the largest size in the habitat where *D. capillaris* was the least abundant (and the *S. flavidulus* density was the highest) (Fig. 3b–c, Supporting information). One likely explanation for this negative density–size relationship in *D. capillaris* is intraspecific competition for resources (White and Harper 1970, Deng et al. 2012, Liu and Pennings 2019). Furthermore, high densities of neighboring *S. flavidulus* may create suboptimal environmental conditions (e.g. shading) that select for a few tolerant *D. capillaris* individuals. These individuals may be able to acquire more resources (because of the lower intraspecific density) and grow to a larger size.

Variation in *D. capillaris* density and size further influenced its prey capture among habitats with varying *S. flavidulus* densities. The number of prey items captured per sundew area was the highest in the habitat with high densities of *S. flavidulus* where *D. capillaris* density was low but each individual was large. Both density- and size-dependent prey capture processes may contribute to this observation. First, intraspecific competition for prey resources among *D. capillaris* individuals is less intense when the intraspecific density is low, allowing each individual to capture more prey items, consistent with our observation of a negative relationship between sundew density and the number of prey items captured per sundew area (Fig. 4c). This is consistent with a previous study on another sundew species showing that prey capture rates decrease with rosette density (Gibson 1991a). Second, if the number of prey items captured is a simple function of trap area, then prey capture per sundew area should be similar regardless of sundew size. Yet, we found that prey capture per sundew area increased with sundew size (Fig. 4d), indicating that size may have a non-linear effect on prey capture ability (e.g. trap attractiveness may increase disproportionately with trap size). Similar patterns have also been reported showing that larger sundew species capture disproportionately more prey items per area compared to smaller species (Krueger et al. 2020). Besides the number of prey captured, sundew size can also affect the size of prey captured, with larger sundew individuals more capable of catching larger prey items because these prey are less likely to escape from larger traps (Gibson 1991b). Moreover, prey-size-weighted capture per sundew area, a proxy for prey resource input, decreased with increasing *D. capillaris* density but increased with increasing *D. capillaris* size (Supporting information). As *D. capillaris* density was lower but its size was larger in the habitat with high *S. flavidulus* densities, this suggests that *S. flavidulus* can potentially benefit prey resource acquisition by co-occurring *D. capillaris*.

Our second proposed mechanism by which the neighboring *S. flavidulus* may influence prey capture by *D. capillaris* is the alteration of insect (prey) communities (Fig. 1). A greater abundance of *S. flavidulus* flowerheads can increase prey availability by attracting more insects, thereby increasing prey capture by *D. capillaris*. However, contrary to our prediction, overall insect abundance was not higher in habitats with higher densities of *S. flavidulus* flowerheads despite higher sundew prey capture in these habitats. Additionally, experimental removal of *S. flavidulus* flowerheads had no apparent impact on insect abundance (Fig. 5a). Furthermore, prey resource availability, as indicated by the insect-size-weighted number from the sticky trap samples, did not vary among the unmanipulated habitats with varying *S. flavidulus* densities and the plots with *S. flavidulus* flowerheads removed (Fig. 5b). The contrasting patterns between prey capture and insect abundance suggest that the observed differential prey capture by *D. capillaris* is not driven by the differences in prey availability among the habitats in our system.

Besides insect abundance, the sticky trap survey showed no major differences in the taxonomic or size composition of insects in the three unmanipulated habitats with varying *S. flavidulus* densities and the plots with *S. flavidulus* flowerheads removed. These observations suggest that *D. capillaris* individuals in different habitat patches may indeed share a common prey resource pool, and that *S. flavidulus* flowerheads may have a little influence on local insect communities, particularly those mobile (Diptera and Hymenoptera) prey that are expected to respond quickly to flowerhead removal. This finding contrasts with a previous study showing that removal of neighboring flowers reduces the number of prey captured by sundew species *D. makinoi* and *D. toyoakensis* (Tagawa et al. 2018). The discrepancy may be due to the differences in the attractiveness of floral neighbors, the overlap in pollinator and prey insect communities, and the interactions between focal and neighboring plants. Still, the taxonomic and size composition of prey captured by *D. capillaris* varied among the habitat types. Smaller *D. capillaris* individuals in the habitats with low and medium *S. flavidulus* densities captured mostly small Diptera prey, whereas larger *D. capillaris* individuals in the habitat with high *S. flavidulus* densities captured not only small Diptera prey but also larger-sized Hymenoptera prey (Supporting information). An explanation for such differences is that prey capture by sundew is mechanically constrained by trap size (Zamora 1990) – small individuals are less capable of retaining larger prey items, whereas larger individuals are able to capture not only more prey items but also larger ones. Differences in prey composition have been documented among sympatric sundew species that vary in size (Krueger et al. 2020), but here we show that within-species size variation may also lead to differential prey capture among conspecific individuals.

In this study, we focused on the influence of biotic interactions on carnivorous plant ecology. However, abiotic factors can play an important role in prey capture as well (Alcalá and Domínguez 2003). It is possible that variation in soil moisture, nutrients and light conditions along the *S. flavidulus* density gradient from the pond edge toward the center may have contributed to the differences in sundew sizes and densities among habitat patches, in turn affecting prey capture performance. However, given the small spatial extent of the density gradient (within three meters), the effects of biotic interactions with *S. flavidulus* may prevail over the effects of these abiotic conditions. Further research manipulating abiotic (e.g. light and water availability) and biotic (e.g. neighboring plant density) conditions is needed to tease apart the direct and indirect effects of abiotic and biotic factors on prey capture by carnivorous plants.

Overall, our results highlight the role of interspecific and intraspecific competition in mediating prey capture in carnivorous plants. Both interspecific (Brewer 2003, 2019) and intraspecific competition (Lam et al. 2018) have been shown to reduce prey capture. Here, we show that interspecific competition from neighbors can be associated with higher prey capture, potentially by reducing intraspecific competition through changes in conspecific density and size. As higher prey resource inputs increase the trap size and seed production of carnivorous plants (Thum 1988, Gibson 1991a), this suggests that neighboring plants may confer fitness benefits to the co-occurring carnivores via increased prey capture. Importantly, this study provides novel insights into how interspecific interactions with heterospecific non-carnivorous neighbors, and intraspecific interactions among conspecific individuals, may together shape prey capture by carnivorous plants.

Acknowledgements – We thank Jennifer Thaler and Anurag Agrawal for the constructive comments on the manuscript.

Author contributions

Gen-Chang Hsu: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Daniel F. Petticord**: Conceptualization (equal); Investigation (equal); Writing – review and editing (equal). **Kelley F. Slimon**: Conceptualization (equal); Investigation (equal); Writing – review and editing (equal). **Jed P. Sparks**: Conceptualization (supporting); Investigation (supporting); Writing – review and editing (supporting).

Data availability statement

Data and code are available from Zenodo: https://doi.org/10.5281/zenodo.14180513 (Hsu et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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