Mitigating the Pollinator-Prey Conflict in *Drosera capillaris*: A Study on Physiological Plasticity and Phylogenetic Conservatism within Drosera

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ABSTRACT

Premise: Carnivorous plants face a dilemma: acquiring nutrients from insect prey while simultaneously relying on insect pollinators for reproduction. Thus, carnivorous plants have evolved mechanisms to avoid/reduce pollinator-prey conflict. This study aims to understand how carnivorous plants deal with this conflict through: macroevolutionary adaptations (floral stalk length) or short-term physiological adaptations, such as modulating trap stickiness. **Methods:** I conducted a field experiment with *Drosera capillaris*, comparing reproductive and non-reproductive plants. I quantified prey capture, counted the number of traps/flowers, and measured adhesive trap strength (stickiness). Additionally, I performed a phylogenetic analysis of 68 *Drosera* species to assess the evolutionary conservatism of floral stalk length. **Results:** Contrary to initial predictions that reproductive plants would reduce trap stickiness to reduce the probability of catching pollinators, these plants exhibited significantly stickier traps than non-reproductive. Despite this increase in adhesive strength, reproductive plants showed a trend toward lower prey capture probability. Phylogenetic analysis revealed high conservatism in floral stalk length across the genus, suggesting that spatial separation is a stable, long-term evolutionary trait. **Conclusions:** This represents a novel, within-species physiological adjustment previously unreported. These findings demonstrate that *D. capillaris* employs a complex, dual strategy to mitigate the pollinator-prey conflict. This combination allows the plant to maximize nutrient acquisition for the high energetic demands of reproduction without jeopardizing pollination success.

Keywords: Pollinator-prey conflict, trap stickiness, physiological plasticity, spatial separation, phylogenetic conservatism

INTRODUCTION

Since Charles Darwin's groundbreaking research (Darwin 1875), carnivorous plants have captivated both scientists and the general public. Carnivorous plants grow in soil that is deficient in nitrogen, phosphorus, and potassium (Ellison 2007). Thus, they have developed mechanisms to obtain nutrients by trapping and consuming animals, such as insects (Behie and Bidochka 2013; Winkelmann et al. 2023). Carnivorous plants use different types of traps to catch prey: snap traps, pitfall traps, and sticky traps. These traps can be considered passive, such as slippery rims, fast-moving traps, or sticky hairs. An evolutionary model proposed by Gibson and Waller (2009) suggests that the main reason fast tentacles/elongated leaves evolved in *Drosera* was because it helped them catch bigger prey. These plants rely on sticky traps to absorb nutrients from an insect prey that was captured; however, they also require insect pollinators to successfully fertilize seeds. This creates a conflict between pollination and prey capture; therefore, carnivorous plants must balance their need for nutrients with their need for reproduction.

Carnivorous plants might resolve the pollinator-prey conflict through two distinct ways. The first is long-term as a macroevolutionary adaptation, where traits, such as spatial separation provided by longer floral stalks, become fixed across a linage to keep pollinators away from the "danger zone". For instance, Anderson (2010) manipulated the flower height in *Drosera cistiflora*, and found that shortened plants received fewer pollinators than plants which were taller in stature. The second is short-term physiological plasticity, where plants actively modulate energetically costly traits, like trap stickiness, based on immediate phenological needs or resource availability. In addition to these two mechanisms, carnivorous plants also evolved other mechanisms, such as phenological differences in flower and trap development (Horner 2014), spatial and temporal separation of flowers and traps (Anderson and Midgley 2001; El-Sayed et al. 2016), trap color (Jürgens et al. 2015; Salces-Castellano et al. 2016), or releasing volatile organic compounds, VOCs (Ojeda et al. 2021). However, the role of trap stickiness in avoiding the pollinator-prey conflict is not known.

Plant reproduction is costly and usually involves trade-offs in terms of energy allocated to other functions such as growth or defense (Herms and Mattson 1991; Obeso 2002). Natural selection should favor traits that help plants avoid the pollinator-prey conflict and maximize the benefit of attracting pollinators to flowers but also attracting prey as food resources. It is expected that carnivorous plants would only attract prey insects to their traps and guide pollinators to their flowers but keep them away from the traps. Thus, plants must modulate their trap stickiness physiology to: (i) produce different levels of trap stickiness when flowering versus non-flowering or (ii) increase floral stalk length to provide greater spatial separation between flowers and traps. If this is true, *Drosera* plants should exhibit different levels of stickiness according to their reproductive phenological state. Also, different *Drosera* species might have evolved different floral stalks lengths, likely to reduce the pollinator-prey conflict.

Although it has been shown there is a potential trade-off between prey capture and pollination, little is known about how *Drosera* plants deal with this conflict. In this study, I examined how these plants have evolved or developed mechanisms: short-term by changing trap stickiness or long-term, how they evolved different flower stalk lengths to prevent it. I tested the following hypotheses: 1) if physical separation is an important and ancestral mechanism for mitigating the pollinator-prey conflict, then floral stalk length will exhibit strong phylogenetic conservatism across the genus Drosera. 2) Because reproduction is energetically demanding, and because fixed traits (like stalk length) cannot respond to biotic and abiotic fluctuations, *D. capillaris* plants will rely on physiological plasticity to mitigate the conflict, producing less sticky traps during the reproductive stage. This study aims to understand how carnivorous plants change trap stickiness and how they evolve longer flower stalks to avoid the pollinator-prey conflict.

MATERIALS AND METHODS

Study site

The research was carried out at Archbold Biological Station, in Florida, USA, in a natural habitat where *D. capillaris* Poir grows. These plants are small, rosette-shaped, perennial insect-eating herbs, commonly found in wetlands, bogs, and marshes in the southeastern United States (Schnell 1976). Although the life cycle of *D. capillaris* is unknown, related *Drosera* species are identified as perennials and are self-incompatible (Stace et al. 1997; Nordbakken et al. 2004). They have multiple red sticky traps for catching prey (Figure 1A-B). The flowers emerge at the center of the rosette, with a long floral stalk extending away from the traps (Fig. 1C). The peak flowering period for this evergreen species is early to mid-spring (April to May). Flowers typically exhibit outcrossing, but they can self-pollinate after closing. Typically, one flower opens per day.

Prey capture and trap stickiness

I collected 19 non-reproductive, and 21 reproductive (with flower buds and at least one flower open) plants in the field and transplanted them into individual containers. Plants were kept at room temperature (26-28 °C) and maintained at 64-67% relative humidity for 12 hours. Under the microscope, I removed all previous prey captured and moved them to the field near the pond for 24 Hrs. Then I estimated the presence/absence of prey, counted the number of preys captured, and counted the number of sticky traps, number of flower stalks, rosette diameter and radius, and measured stickiness of the traps. To obtain the rosette area, I used the formula to calculate the area of a circle: $A = \pi * \text{radius}^2$.

To measure the stickiness of the traps I placed a 1x1 cm filter paper square to the traps attached with thread to a paper basket. Then, I slowly added sand to the basket until the filter paper detached from the trap. Using a weigh gram scale (100g ± 0.01g), I measured the weight of sand as a direct measurement of plant stickiness. Then using this weight, I obtained the force in Newtons necessary to detach the filter paper using the formula: $N = (\text{Weight (g)} / 1000) * 9.81$, where 9.81 is the gravity force. The filter paper was replaced with each plant examined.

Phylogenetic analysis and floral stalk length evolution

To understand the evolution of floral stalk length in the *Drosera* genus, I conducted an examination of digital specimens from iDigBio (www.idigbio.com), and GBIF. Based on the photos available, I measured the floral stalk length of 68 *Drosera* species, measuring 1-4 floral stalks using ImageJ (Schneider et al. 2012). I reconstructed a phylogenetic hypothesis of this group using sequence data from the *rbcl* plastid gene obtained from NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/) and aligned using MAFFTpy using the "Auto" strategy that selects the best one according to each individual sequence (Vences et al. 2022). The best-fit scheme was the GTR+G substitution model, according to partitionFinder (Lanfear et al. 2017). Phylogenetic reconstruction and divergence time estimation was were conducted in BEAST v2.7.7 (Drummond and Bouckaert 2015) using an Optimized relaxed molecular clock, GTR substitution model and a calibrated Yule model. I included one calibration point for the *Drosera* node using a normal distribution: 36 Ma [95% CI: 49.5-26] according to Sen *et al.* (2020). One independent MCMC run was conducted for 208 million generations, sampling every 5,000 steps. After checking stability, the adequate effective sample size (ESS > 200) and determining burn-in values (10%) in

Tracer v1.7.2 (Rambaut et al. 2018), the two independent runs were merged using LogCombiner after exclusion of burn-in trees (20838 trees). Then, I inferred the maximum clade credibility tree with TreeAnnotator v2.7.6 (Heled and Bouckaert 2013).

I tested for a phylogenetic signal in floral stalk length using Pagel's λ (lambda; Pagel, 1999), calculated with the phylosig() function implemented in phytools (Revell 2024). A lambda $(\lambda) \approx 0$ indicates low/weak phylogenetic signal; lambda $(\lambda) \approx 1$ indicates a strong phylogenetic signal. I mapped the ancestral reconstruction of floral stalk length across the phylogeny using the contMap function using phytools (Revell 2024).

Statistical analysis

I fitted two Generalized Linear Models (GLM): 1) To examine the prey capture probability, I performed a logistic regression in R using a binomial distribution and “probit” as link function (lower AIC, "logit”). I used trap stickiness, the number of traps, phenological state, and mean floral stalk length as explanatory variables. I also included the interaction between stickiness and phenological state, and number of traps and phenological state. 2) To analyze the stickiness force, I performed a Generalized Linear Model using a Gaussian distribution and “log” as link function. I used the number of traps, phenological state, and mean floral stalk length as explanatory variables. To find the best model, I performed a stepwise model selection by AIC using the function stepAIC in MASS package (Venables and Ripley 2002). Then, I checked the goodness of fit of the models using the scaled residuals created with the r package DHARMa (Hartig 2018). I generated the plots using ggeffects (Lüdecke 2018) and ggplot (Wickham 2016) in R. Pairwise comparisons were done using the emmeans package (Lenth 2016).

Structural equation models (SEM): I used Structural Equation Modeling (SEM) to assess the relationships between plant morphology, on prey capture probability, and trap stickiness. The initial full model included three response variables: prey capture probability, trap stickiness, and floral stalk length. The explanatory variables were number of traps per plant, number of floral stalks per plant, and plant rosette area. The full model included interactions between plant traits, as well as covariance terms to account for potential correlations among response variables. Model selection was performed iteratively by removing non-significant terms based on p-values ($p > 0.05$), while prioritizing biological interpretability. The final model was chosen based on the AIC, the chi-square test, the comparative fit index (CFI), Tucker-Lewis index (TLI), root mean square error of approximation (RMSEA), and standardized root mean square residual (SRMR), ensuring that it met standard thresholds for good model fit ($CFI > 0.95$, $RMSEA < 0.08$, $SRMR < 0.08$). SEM was fitted using maximum likelihood estimation (ML) in the *lavaan* (Rosseel 2012) package in R. Visualization of the SEM models was created using *semPlot* (Epskamp 2015) and *CorelDRAW* (Corel Corporation).

RESULTS

I found that most common insects trapped by *D. capillaris* were flies (Diptera), spiders and aphids. There was a nearly significant effect for differences in the prey capture probability between reproductive and non-reproductive plants ($X^2 = 3.34$, $p = 0.06$; Table S1), in which there is a trend of a higher prey capture probability in non-reproductive plants than reproductive plants ($z = 1.69$, $p = 0.09$; Figure 2A). Floral stalk length and stickiness were not statistically significant for the prey capture probability. There was a significant effect of the number of traps on the prey capture probability ($X^2 = 4.1$, $p = 0.043$; Table S1).

Trap stickiness

There was a significant effect of phenological state on trap stickiness ($X^2 = 12.86$, $p <0.001$; Table S1), there was a higher stickiness in traps from reproductive plants than from non-reproductive plants ($t = -3.74$, $p < 0.001$, Figure 2B). However, floral stalk length was not statistically significant. There was a significant effect of the number of traps on the trap stickiness ($X^2 = 7.60$, $p = 0.006$; Table S1).

Structural equation models (SEM)

The SEM showed excellent fit to the data (χ^2 (3) = 0.408, $p = 0.9$; $CFI = 1.000$; $TLI = 1.113$; $RMSEA < 0.0001$; $SRMR = 0.021$), indicating that the proposed model accurately represents the relationships among variables. Overall, SEM model explained 84% of prey capture probability, 19% of trap stickiness, and 32% of floral aperture (Figure 3; Table S2). Prey capture probability was positively associated with the number of traps ($\beta = 1.154$, $p < 0.001$) and negatively associated with the number of floral stalks ($\beta = -0.609$, $p < 0.001$) and plant size ($\beta = -0.429$, $p < 0.001$). Trap stickiness showed a negative relationship with the number of traps ($\beta = -0.438$, $p = 0.019$) and a positive relationship with the number of floral stalks ($\beta = 0.569$, $p = 0.002$). The number of traps had a strong positive effect on floral stalk length ($\beta = 0.567$, $p < 0.001$), whereas plant size had no significant effect (β = 0.086, p = 0.574). Finally, trap stickiness did not significantly affect prey capture (β = -0.102, p = 0.124), and plant size had no effect on floral stalk length (β = 0.086, p = 0.574). Covariances between response variables were also non-significant.

Phylogenetic analysis

The phylogenetic analysis recovered a well-resolved tree topology with high statistical support for most nodes (likelihood = -6530.367, ESS = 10274). The marginal likelihood of the BEAST analysis was estimated at -6856.5261, and all key parameters showed satisfactory mixing and convergence, with ESS values exceeding 200 (ESS > 500 for most parameters). The recovered relationships are largely consistent with previous phylogenetic studies of the group (e.g., (Rivadavia et al. 2003)). Posterior probabilities were ≥0.90 for 54.93% of the internal nodes, indicating strong support (S1 Fig 1). The divergence of *Drosera* was estimated at 35.196 Ma (95% HPD: 45.05–25.22 Ma), consistent with the fossil calibration used. These results provide a robust temporal framework for understanding the evolutionary history of the group.

Floral stalk length evolution

For the *Drosera* genus floral stalk length exhibited high levels of trait conservatism (Pagel's λ = 0.716, p-value < 0.001, Figure 4). Based on this result, more closely related species tend to have similar floral stalk length. There were some species that exhibited similar lengths, suggesting that this trait is phylogenetically conserved.

DISCUSSION

This study aimed to test how carnivorous plants mitigate the pollinator-prey conflict through morphological and physiological traits. The results of this study support hypothesis 1, high Pagel's λ, demonstrate that more closely related species tend to have similar floral stalk lengths, reflecting high evolutionary trait conservatism. However, hypothesis 2 is rejected, I found higher stickiness in traps from reproductive plants than from non-reproductive plants.

The results of this study suggest that *D. capillaris* mitigates the pollinator-prey conflict not through an isolated mechanism, but rather through a complex, adaptive strategy that integrates macroevolutionary stability with microecological flexibility. On a long-term evolutionary scale, the strong phylogenetic signal demonstrates that floral stalk length is a highly conserved, fixed morphological trait across the genus. This stable spatial separation acts as a reliable physical barrier, isolating the blooming flowers from the "danger zone" of the sticky traps. This morphological separation strategy has effectively protected pollinators preventing them from getting trapped and digested. Consequently, *D. capillaris* relies on a second, short-term phenology-linked physiological adjustment, making its traps much stickier right when the plant starts to produce their flowers. By maintaining consistently long floral stalks alongside these flexible, short-term increases in trap stickiness, the plant can safely enhance its resource acquisition to meet the energetic demands of reproduction, successfully balancing nutritional needs with reproductive fitness in nutrient-poor environments. This idea is supported by Thorén et al. (2003), they showed that in *Drosera rotundifolia* plants can modify trap stickiness in response to resources available, demonstrating that trap stickiness is a plastic trait. These mechanisms appear to be very effective at reducing the likelihood of trapping pollinators. Actually in many *Drosera* species, very few pollinators actually end up as prey, evidence that these plants generally spare their pollinators efficiently (Anderson 2010; Horner 2014; El-Sayed et al. 2016). This study supports that pattern: flowering plants captured fewer insects, consistent with the idea that these carnivorous plants reduce their trapping activity when pollinators are around.

Previous studies have extensively documented spatial, temporal, and visual/olfactory mechanisms that carnivorous plants use to reduce the pollinator-prey conflict (Jürgens et al. 2015; El-Sayed et al. 2016; Salces-Castellano et al. 2016; Ojeda et al. 2021). However, the stickiness of the traps, as a mechanism to prevent prey-pollinator conflict, is a novel insight regulating pollinator-prey interactions. The role of trap adhesive strength (trap stickiness) has not been considered as a factor in this conflict. In this study I predicted that, due to the high energetic costs associated with reproduction and to avoid/minimize the pollinator-prey conflict, plants in the reproductive phenological state would invest less resources in trichomes (stickiness) production. Thus, *Drosera* plants will produce less sticky traps, capturing fewer prey than non-flowering plants, as SEM results shown. Contrary to this prediction, I found that reproductive plants had stickier traps than non-reproductive plants, but they captured less prey.

Another possible explanation is that *D. capillaris* may reduce pollinator capture by using other cues that attract insects, such as smells or visual cues. For instance, many *Drosera* species have white or brightly colored flowers to attract pollinators, but at the same time their red sticky traps lure other small insects (El-Sayed et al. 2016). *D. capillaris* fits this profile, white flowers and red traps, so it likely spares pollinators through visual signals rather than by decreasing trap stickiness. Also, it is likely that *D. capillaris* relies on differentiation of VOCs between flowers and traps to mitigate pollinator-prey conflict. Previous studies have shown that carnivorous plants release different VOCs for flowers and traps, with flowers attracting pollinators and traps attracting preys (El-Sayed et al. 2016). Analyzing the visual cues and VOC profiles of flowers and traps would help clarify the role of these traits in reducing pollinator-prey conflict.

In conclusion, this study demonstrates that *D. capillaris* solves the pollinator-prey conflict through a complex adaptive strategy, involving a macroevolutionary strategy and a short-term physiological plastic adaptation, significantly increasing the adhesive strength of its traps during their reproductive stage. By coupling these two strategies plants can safely maximize their nutrient acquisition to meet the energetic demands of reproduction without jeopardizing its pollination success.

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AUTHOR CONTRIBUTIONS

Material preparation, data collection and analysis were performed by Mario A. Sandoval Molina. The first draft of the manuscript was written by Mario A. Sandoval Molina and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability

All data, gene alignment, phylogenetic tree have been deposited to Harvard Dataverse (https://doi.org/10.7910/DVN/01J2OX).

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Figure 1. *Drosera capillaris*. A) This panel displays the sticky trichomes that the plant uses to trap prey. B) An arthropod captured and digested by enzymes produced in the sticky trichomes. C) The spatial separation between the flower and the sticky traps.

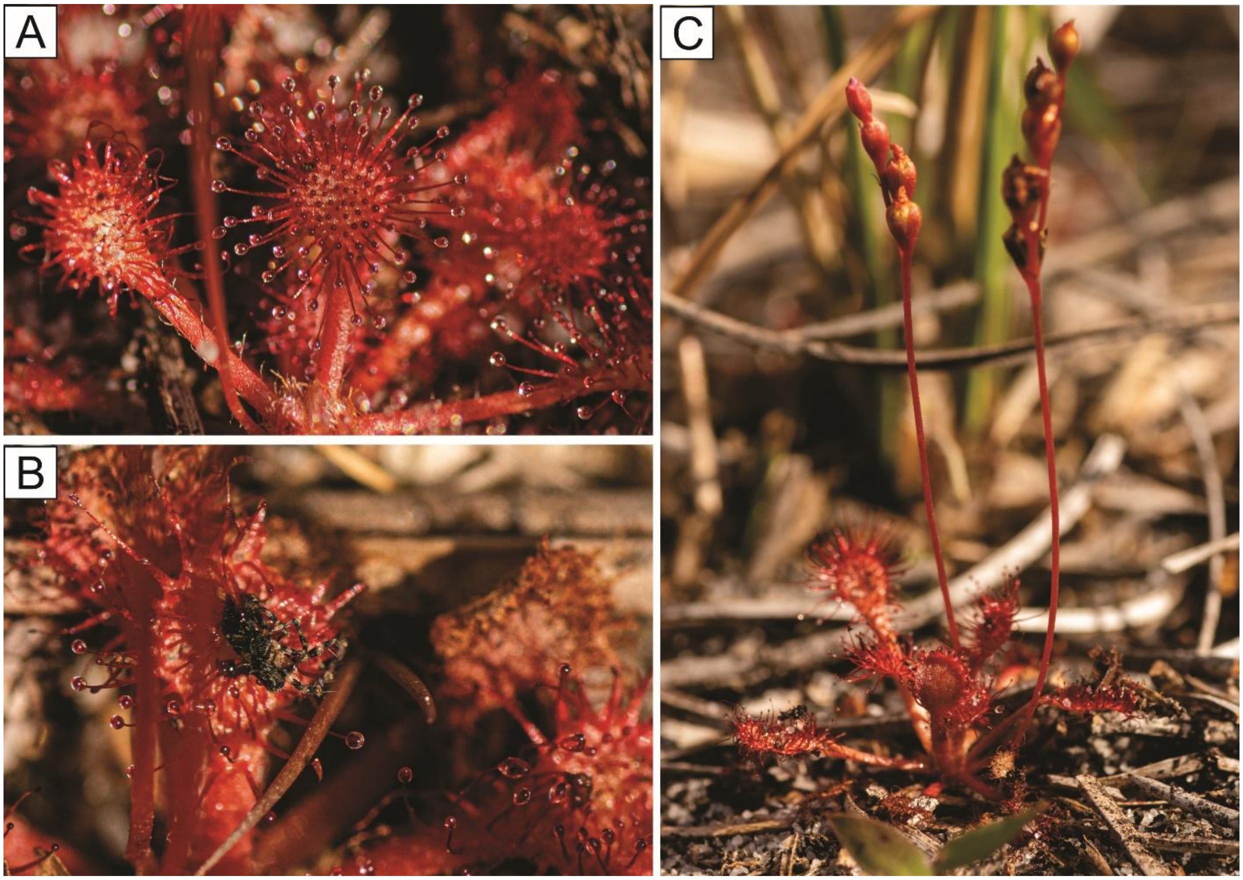


Figure 2. The effect of phenological state on A) prey capture probability and B) trap stickiness in *Drosera capillaris*. P-values were calculated with Tukey post hoc comparison.

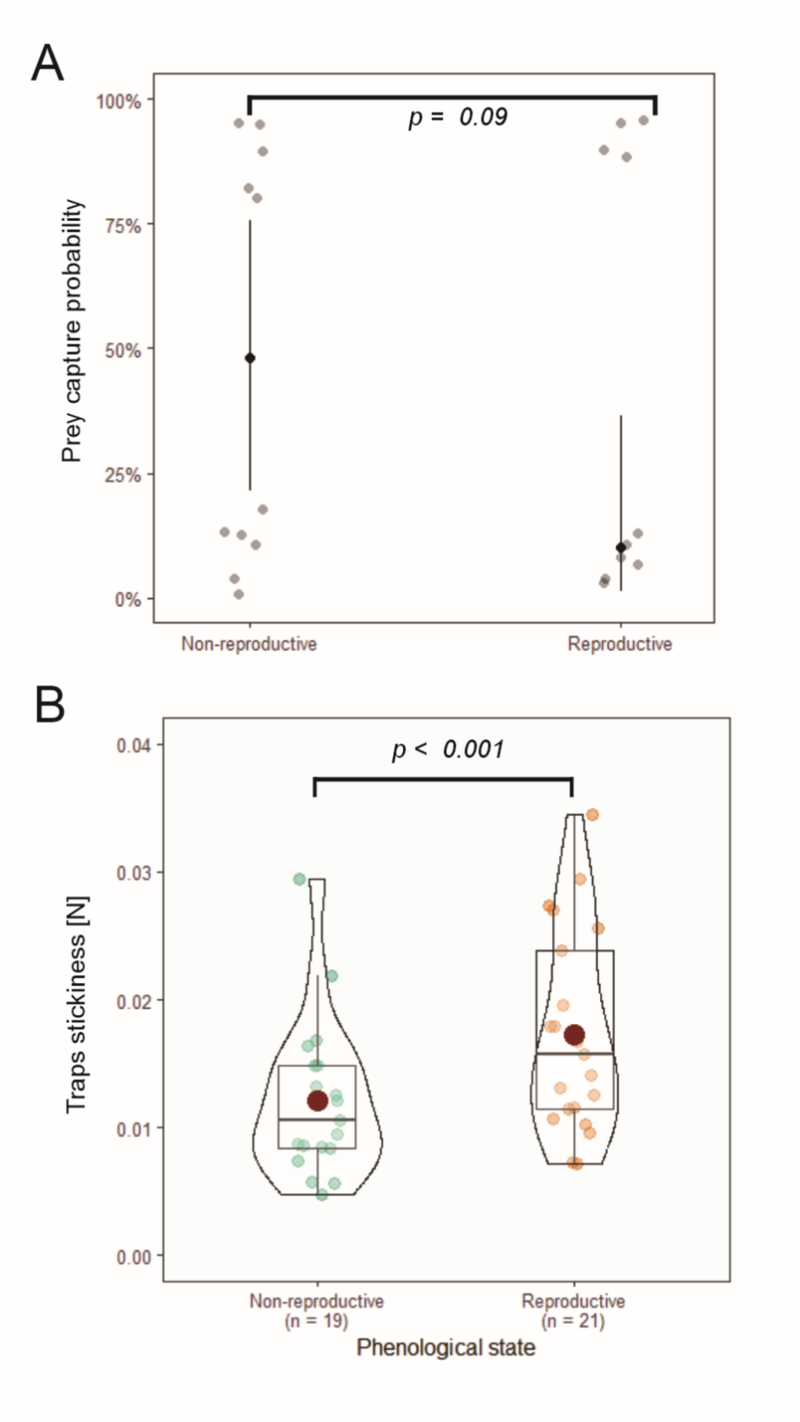


Figure 3. Structural equation models (SEM) showing the relationships among number of traps, number of floral stalks, and rosette area on prey capture probability, trap stickiness, and floral stalk length. Green solid lines represent positive effects, whereas red dashed lines indicate negative effects. Dotted lines on top represent the positive relationship between explanatory variables. Numbers by the arrows represent standardized path coefficients. R-squared for each component in the model is given inside the box. Significance: *P < 0.05, ** P< 0.01, and *** P< 0.001.

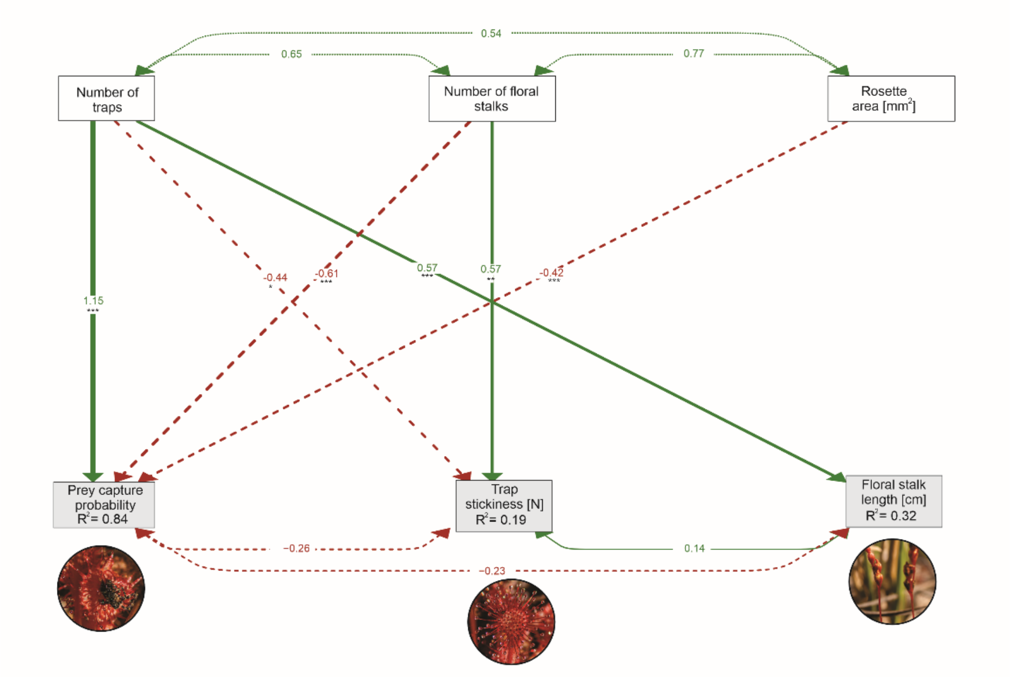
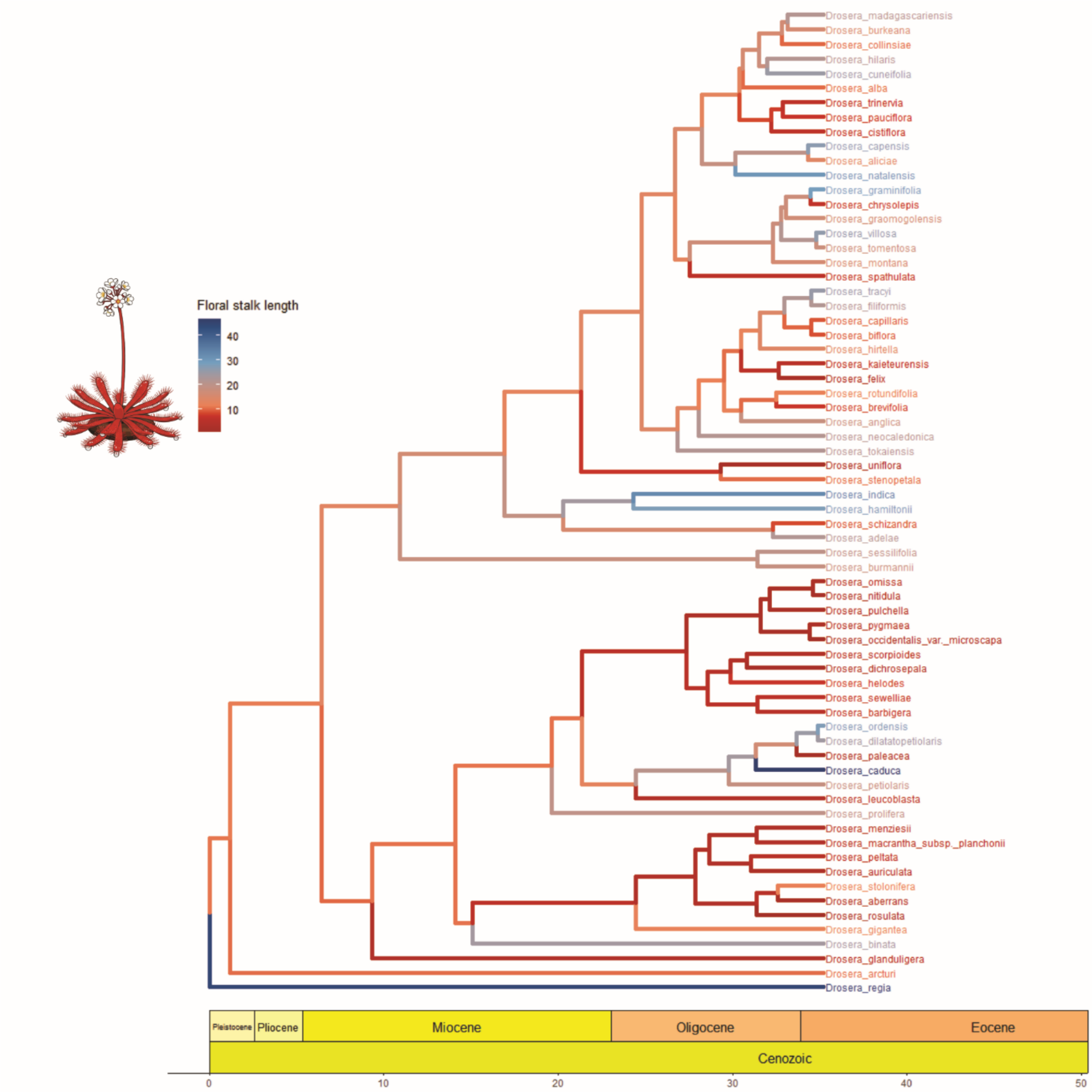


Figure 4. Floral stalk length measured from digitalized specimens and mapped onto the phylogenetic tree of Drosera using floral stalk length means. The shading in the branches represents the reconstruction of the traits, with colder colors indicating higher trait values and warmer colors indicating lower trait values. Lambda (λ) values are also included.



Supplementary information:

Mitigating the Pollinator-Prey Conflict in *Drosera capillaris*: A Study on Physiological Plasticity and Phylogenetic Conservatism within Drosera

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Table S1. Effect of number of flower stalks, number of traps, and phenological state on prey capture probability and trap stickiness in *Drosera capillaris*. Significance levels of the reduced models were calculated with an Analysis of Deviance Table (Type III tests).

Prey capture probability

Variables	*LR.Chisq*	*DF*	*P.value*
Number of traps	4.10	1	0.043 *
Phenological state	3.34	1	0.068 .

Trap stickiness

Variables	*LR.Chisq*	*DF*	*P.value*
Number of traps	7.60	1	0.006 **
Phenological state	12.86	1	<0.001 ***
Floral stalk length	0.28	1	0.598

*<0.001 '***' 0.001 '**' 0.01 '*' 0.05 '.'*

Table S2. Results of the best structural equation model (SEM) showing the relationships among number of traps, number of floral stalks, and plant rosette area on prey capture probability, trap stickiness, and floral stalk length.

Response variable		*Explanatory variable*	*estimate*	*Std. error*	*z-value*	*p-value*	*std.lv*	*std.all*
Prey capture probability	~	Number of traps	0.16	0.01	13.97	<0.001	0.16	1.15
Prey capture probability	~	Number of floral stalks	-0.08	0.01	-5.73	<0.001	-0.08	-0.61
Prey capture probability	~	Plant rosette area	-0.06	0.01	-4.57	<0.001	-0.06	-0.43
Trap stickiness	~	Number of traps	-0.44	0.19	-2.34	0.02	-0.44	-0.44
Trap stickiness	~	Number of floral stalks	0.57	0.18	3.06	<0.001	0.57	0.57
Floral stalk length	~	Number of traps	0.57	0.13	4.36	0.00	0.57	0.57
		Covariances						
Response variable		*Explanatory variable*	*estimate*	*Std. error*	*z-value*	*p-value*	*std.lv*	*std.all*
Prey capture probability	~~	Trap stickiness	-0.01	0.01	-1.58	0.11	-0.01	-0.26
Prey capture probability	~~	Floral stalk length	-0.01	0.01	-1.44	0.15	-0.01	-0.23
Trap stickiness	~~	Floral stalk length	0.10	0.12	0.90	0.37	0.10	0.14

Response variable	R^2
Prey capture probability	0.84
Trap stickiness	0.19
Floral stalk length	0.32

Fig S1. Posterior probability support across the *Drosera* phylogeny. A total of 54.93% of internal nodes showed posterior probabilities ≥0.90, indicating strong nodal support.