

A Nectar-Inhabiting Bacterium May Not Influence Female Fitness in *Ipomopsis aggregata*

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Abstract

Hummingbirds are known to select which floral resource to utilize based on visual and olfactory cues. The role that microbes play in mediating the mutualism between hummingbirds and flowers is mostly unexplored in the field of microbial and pollination ecology. Bee pollinators are known to be deterred by high concentration of bacterial nectar, and the same has been shown for hummingbirds but only in one highly controlled setting with artificial flowers. There is limited evidence on how bacterial nectar influences hummingbird pollination, especially in wild systems. We tested if the presence of *Pantoea sp.*, a plant generalist bacterium, in floral nectar influences the female fitness of *Ipomopsis aggregata*, a hummingbird-pollinated wildflower. Plants were inoculated with sterile or bacterial nectar, at the end of the growing season, seed set, fruit set, and fly larval predation were calculated to test the effects of bacterial nectar on plant fitness. Floral and vegetative plants were also accounted for in our fitness models. We found no significant differences in seed set, fruit set, or predation between our *Pantoea*-treated plants and sterile nectar treatments. We found that larger floral and vegetative traits of *I. aggregata* were associated positively with seed set and predation, but not fruit set. Pollen limitation was found to be minimal or absent, hand pollination did not prove to significantly improve seed or fruit production. Hummingbird pollination or female fitness of *Ipomopsis aggregata* was not affected by *Pantoea sp.* in floral nectar in field realistic conditions. Plant morphology was found to play a more important role in reproductive success than microbial nectar dynamics. These results suggest that microbial mediation of plant-pollinator mutualisms may be context-dependent and not universally disruptive.

Introduction

Plant-pollinator mutualisms are highly necessary for economic and ecosystem services; they provide enhanced reproduction in flowering plants, higher seed set, and fruit yield (Otieno, 2020). Bird pollinators and specifically hummingbirds, are important mutualists in plant-pollinator systems. Hummingbird-pollinated plants have significantly increased seed set and germination rates compared to plants pollinated by other pollinators, particularly when plants require cross-pollination (Abrahamczyk et al., 2025). Hummingbirds respond to visual, gustatory, and possibly olfactory cues to decide which flowers to feed from. Understanding the factors mediating hummingbird visitation in plant-pollinator mutualisms is important as these interactions not only influence individual plant fitness and reproductive success, but also mediate biodiversity patterns and the stability of ecosystems (Irwin & Brody, 1998).

Mutualisms rarely are composed of only two species, with three or more often participating (Palmer et al., 2010). These mutualistic systems are highly prone to exploitation, where one member can receive benefits while giving none in return. An example of exploitation in plant-pollinator mutualisms is nectar robbing behavior, where a floral visitor consumes nectar without providing pollination. It is known that bee pollinators can exhibit nectar robbing behavior; where pollinators extract nectar from flowers by chewing through the flower's base with their mandibles (Irwin et al., 2010). This practice in some instances is more efficient for the pollinators than legitimate pollination. *Ipomopsis aggregata* (Polemoniaceae) is a flowering plant native to Colorado that experiences both hummingbird pollination and nectar robbing from bees (Irwin & Brody, 1998). It is known that hummingbirds rely on gustatory cues to determine which flowers to visit based off sugar content (Rankin et al., 2018), but whether hummingbirds rely on olfactory cues for decisions on flower visitations is debated (Kim et al., 2021; Núñez et al., 2021). Hummingbirds also rely heavily on visual cues, being able to avoid *Ipomopsis aggregata* flowers that have less nectar from simulated robbing (Irwin, 2000). Nectar robbing has been shown to have a neutral to negative effect on hummingbird pollination (Irwin & Brody, 1998).

It is unclear if that hummingbirds can detect microbial content by smell, but gustatory cues such as sugar and amino acid concentrations as well as dissolved microbial metabolites may all be factors contributing to the decision of flower visitation. When bee pollinators rob a flower

of its nectar, they can inoculate the nectar with microbes (Morris et al., 2020). The hole that is left after nectar robbing also provides a gateway for generalist epiphytic microbes to inoculate the nectar of flowering plants. Nectar-inhabiting bacteria are known to have deleterious effects on plant-pollinator interactions. Some effects include decreased seed production, and pollinator visitation, increased pH levels, and sugar content. For example, the nectar specialist bacterium *Neokomagatea sp.* has been shown to reduce pollination by 23%, seed production 18%, and nectar consumption from hummingbird pollinators by 27% (Vannette et al., 2013). The generalist plant bacterium *Pantoea ananatis* has been shown to deter honey bees (*Apis mellifera*) when at high concentrations in nectar (Scheiner et al., 2020). This suggests that bacteria can disrupt plant-pollinator mutualisms, including hummingbird-plant mutualisms, resulting in a decrease in female plant fitness.

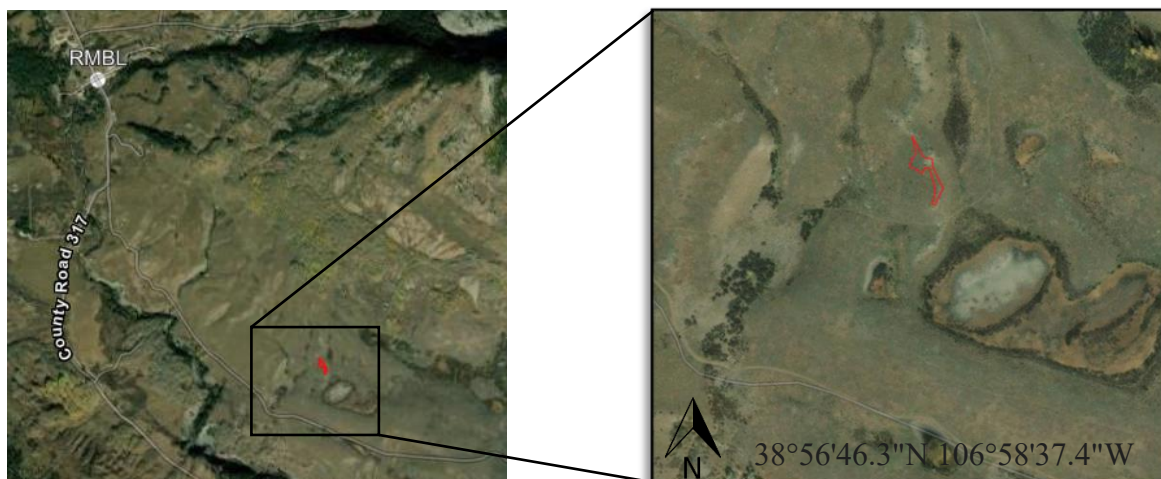
Not much is known about how generalist plant-associated bacteria of the *Pantoea* genus play a role in mediating hummingbird pollination on the Colorado native, hummingbird-pollinated plant, *Ipomopsis aggregata*. Bacteria of the genus, *Pantoea*, are commonly found on the leaves, fruits, and seeds of many plant species (Walterson & Stavrinos, 2015). Here, we will test the hypothesis that the presence of the bacterium *Pantoea sp.* in the nectar of *I. aggregata* will negatively affect the mutualism between hummingbirds and *I. aggregata*. To test this, we will assess the female fitness of *I. aggregata* that has been treated with a nectar solution containing field-realistic amounts of *Pantoea sp.* Seed and fruit set will be used as measures of fitness in *I. aggregata*. Analyzing female fitness allows us to directly quantify hummingbird pollination as *I. aggregata* is mainly pollinated by hummingbirds. Comparing the number of seeds from treated plants and control plants gives us a direct measure of which plants were visited and pollinated by hummingbirds more than others.

Methods

Study System

All work for this project was done north of the first bend of Deer Creek Trail (38°56'46.3"N 106°58'37.4"W) at the Rocky Mountain Biological Laboratory, near Crested Butte, Colorado. The elevation for this site is approximately 2900 m. We studied multiple focal species participating in the hummingbird-pollination mutualism, the first of which is *Ipomopsis aggregata*, a biennial flowering plant belonging to the phlox family which is native in the

southern Colorado Rockies (Tilley & Aberdeen, 2017). This species is mainly pollinated by hummingbirds (Campbell et al., 1991), the salverform shape of the corolla prevents native bee species from entering the opening to forage. Our focal pollinator species we are studying is *Selasphorus platycercus*, also known as the broad-tailed hummingbird. Characterized by their iridescent green feathers, these hummingbirds serve as the main species that mediate reproduction for *I. aggregata*. *S. platycercus* almost always act as legitimate pollinators for *I. aggregata* and rarely, if ever act as secondary robbers (Irwin & Brody, 1998). For our bacterial inoculant, used *Pantoea* sp. *Pantoea* is a gram-negative, plant generalist bacteria that is found on the leaves and fruit of various plants, vegetables, and grains (Morin, 2014). It is thought that *Pantoea* sp. enters the nectar via wind or rain dispersal through robbing wounds, which are located within 1-2 mm of the nectary. The specific strain of *Pantoea* sp. we will be using as a nectar inoculant was isolated from an *I. aggregata* flower that was robbed by a single *Bombus bifarius* queen at the Deer Creek Trail site (38°56'46.3"N 106°58'37.4"W). Using Sanger sequencing of the 16S rRNA gene, we were able to identify our bacterium as *Pantoea* sp. Around 400 bp portions of the highest quality region of the 16S gene were obtained from both forward and reverse reads. The resulting sequences were analyzed using NCBI BLAST, with the search restricted to 16S ribosomal RNA genes from Bacteria and Archaea type strains. Both forward and reverse sequences resulted in a 100% match to multiple *Pantoea* species including *Pantoea agglomerans*, *Pantoea eucalypti*, and *Pantoea brenneri*. Due to the inability to distinguish among these closely related species, we will refer to our strain as *Pantoea* sp.



Hypothesis

Not much is known about how hummingbirds chose which floral resource to forage from. As discussed earlier, it is known that hummingbirds use visual and gustatory cues to decide which flowers to feed from, being able to avoid flowers with no nectar (visual) and determine which nectar resource is most valuable based on sugar content (gustatory) (Irwin & Brody, 1998). It is unclear whether hummingbirds can see or taste which flowers are infected with bacteria. It has been shown that hummingbirds are averse to artificial flowers containing nectar inoculated with a nectar-specialist bacterium (*Neokomagatea* sp.), and that bee pollinators avoid different nectar microbes in the *Pantoea* species. We predict that hummingbirds will be averse to flowers with *Pantoea* sp. inoculated nectar. This should result in lower female reproductive fitness, categorized by lower fruit formation, and seed set.

Experimental Design

We manipulated the nectar microbial communities and pollination treatments of *Ipomopsis aggregata* flowers. A total of four treatments were used: 1) Bacterial nectar analog treatment, 2) Sterile nectar analog treatment, 3) Hand-pollinated control, 4) and an open-pollinated control. Our experimental treatments (bacterial nectar and hand pollinated) had 35 replicate plants and our controls (synthetic nectar and open pollinated) have 30 replicates, totaling 120 total plant replicates. Previous studies have shown that our sample size should be sufficient to test the effects of our treatments on female reproductive fitness in *I. aggregata* (Irwin & Brody, 1998). Every three days (Monday, Wednesday, and Friday) our bacterial treatments were inoculated across all open flowers per *I. aggregata* individual. The same was done for our sterile artificial nectar on separate marked plants. The same timeline was followed for our hand pollinated treatment, anthers were taken from other nearby non-treated *I. aggregata* and using forceps, were applied to the stigmas of our treated plants to provide supplemental pollination. The open pollination treatments were not modified in any way. The female reproductive success of the open pollination was then compared to that of the hand-pollinated controls to determine the effects of pollen limitation on the female fitness of *I. aggregata* in Deer Creek. Afterwards, fruit and seed set will be analyzed to determine *Pantoea* sp. effects on *I. aggregata* female fitness.

Plant protocols

120 *I. aggregata* in our study site will be randomly selected and individually assigned to one of our treatment groups. Each plant will be tied to a plant support stake to best avoid herbivory by deer. Each plant stake is labeled with identification cards at the base and colored flags at the top of the stake, corresponding to the treatment type. The colors red, orange, and pink are avoided in our stake flags to avoid any additional attraction of hummingbirds (O'Connor, 2017). Plant height, root width, and corolla length and width will be measured, as these traits are known to influence hummingbird pollination of *Ipomopsis* (Campbell et al., 1991).

Microbial and artificial nectar

A nectar analog mimicking the natural sugar and amino acid concentrations of *Ipomopsis aggregata* nectar (Valerie Martin, unpublished data) was formulated in the lab and filter-sterilized using a 0.2 μm filter. After preparation of the nectar analog, it is stored at -80 °C until use. To make the *Pantoea*-inoculated nectar, two-day *Pantoea sp.* cultured on Luria-Bertani agar is added to the nectar analog at an optical density at 360 nm of 0.02-0.04 (corresponding to field-realistic nectar bacterial densities; Valerie Martin, unpublished data). This bacterial solution is then incubated at 20 °C for 2 days before being used for treatment.

Bacterial inoculation and synthetic nectar treatment

Using a Hamilton syringe, across each flower per plant, 1 μL of synthetic nectar or bacterial inoculant (treatment dependent) will be deposited at the back of each *I. aggregata*. In between plants, the syringe will be cleaned and wiped with 70% ethanol to prevent bacterial contamination and cross pollination.

Hand pollination controls

Anthers were collected from multiple nearby non-treatment *I. aggregata* plants. Using forceps, the collected anthers are rubbed on to all visible stigmas protruding from the individual hand-pollination *I. aggregata* plants in this treatment. Sufficient pollination is achieved once there is visible pollen on the stigmas (McGrady et al., 2020). A hand pollination treatment is important for this project as it tests the effect of pollen limitation on plant fitness when compared to controls.

Open pollination controls

Besides the protocols described in plant protocols, no experimental procedures were conducted on these treatment plants. This serves as our control for bacterial and synthetic nectar treatments, but also for our hand pollination treatments to measure the effects of pollen limitation on female fitness.

Statistical Analysis

Trait Analysis

We ran several different statistical tests and models to determine plant traits effects and our experimental treatments effect on female fitness in *Ipomopsis aggregata*. When testing how our plant traits differed by treatments, we ran Kruskal Wallis tests, if we found significance, we followed with a pairwise Wilcoxon test to determine where the significant effect arose. Shapiro–Wilk tests were used to assess normality prior to choosing non-parametric methods. We also conducted Pearson correlations among key plant traits, and due to high multicollinearity, we used principal components analysis (PCA) to reduce trait dimensionality. Floral traits (PC1_flowers) and vegetative traits (PC1_traits) were each reduced to a single principal component using scaled and imputed trait data. Both PCAs were weighted negatively, when plotted this means as the x-axis becomes more negative, the flower or individual plant grows larger.

Fitness Measurements

To measure female reproductive fitness in *I. aggregata*, we analyzed fruit set, seed set, and predation. For fruit set, we collected and counted all viable fruits and then divided them by the number of possible fruits. Possible fruits were calculated by adding all fruit aborts with total number of viable fruits. We then counted all the seeds per plant and averaged the number of seeds per fruit and then extrapolated out to the number of total fruits. Total predation was the count of fly larvae per plant.

Trait-Fitness Relationships

Generalized linear models were used to test the associations between plant/floral display size (PCAs) and each fitness metric. For seed set and total predation, we used negative binomial distribution for our GLM due to over dispersion in our dataset. Fruit set fell between 0 – 1 for all values so we tested the association with floral and fitness metrics using quasibinomial distributed GLMs.

Pollen Limitation

To determine the amount of pollen limitation, we compared to average seed set and fruit set between hand-pollinated and open-pollinated plants. Below is the equation used to calculate pollen limitation for both seed and fruit set.

$$\text{Pollen Limitation} = 1 - \left(\frac{\text{Open Mean}}{\text{Hand Mean}} \right)$$

Separate calculations were made for both seed set and fruit set.

Treatment Comparisons

To evaluate the effects of pollination and microbial inoculation treatments on reproductive success, we compared seed set, fruit set, and total predation across treatment groups. When data were non-normally distributed (confirmed via Shapiro–Wilk tests), we used non-parametric Wilcoxon rank-sum tests (for two-group comparisons) or Kruskal–Wallis tests (for more than two groups). Pairwise comparisons following Kruskal–Wallis tests were conducted using Wilcoxon tests with Benjamini-Hochberg (BH) correction for multiple testing were used if we found significance in the Kruskal-Wallis tests. To further test the interaction among plant traits and experimental treatments, we fit generalized linear mixed models (GLMMs) using the glmmTMB package in R. We had our treatments and plant/floral trait PCAs as fixed effects and used the correct dispersion depending on how our data was distributed for our dependent variables.

All model residuals were validated using the DHARMA package in R and overdispersion was tested with `testDispersion()` in the software R.

Results

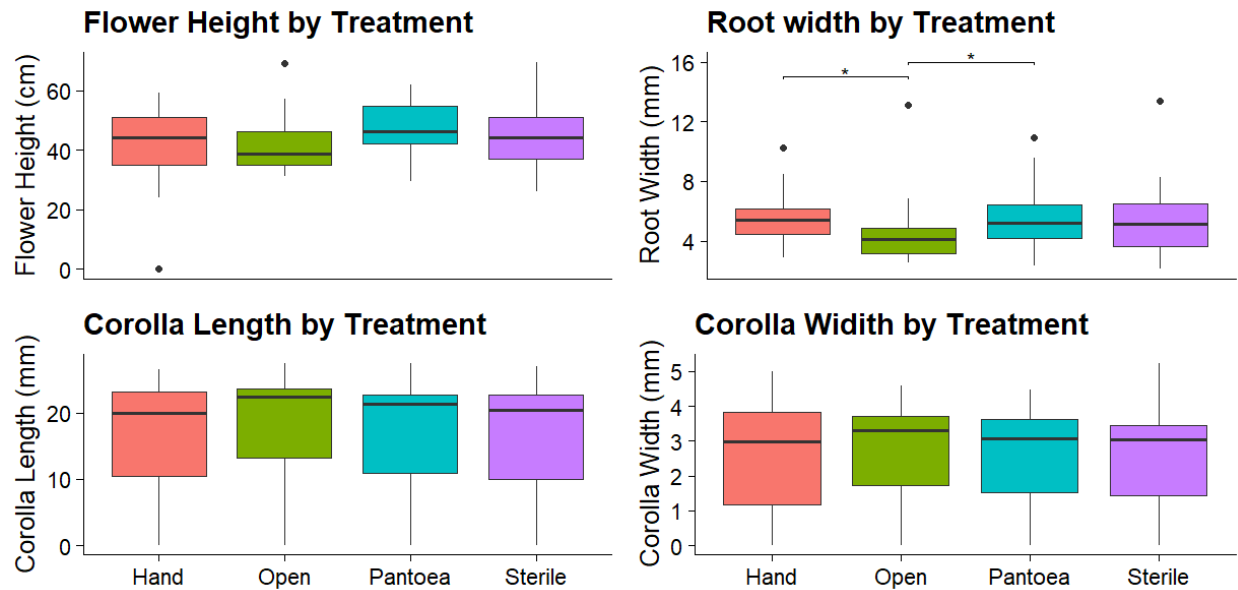


Figure 1. Plant Traits by Treatment

- a) Flower Height by Treatment. ($p = 0.09$, $H = 6.44$, $df = 3$)
- b) Root Width by Treatment. ($p = 0.04$, $H = 7.94$, $df = 3$)
- c) Corolla length by Treatment. ($p = 0.59$, $H = 1.89$, $df = 3$)
- d) Corolla width by Treatment. ($p = 0.54$, $H = 1.29$, $df = 3$)

Between our plant traits, there was only a significant difference between treatments in our root width measurements. The hand pollinated ($p = 0.42$) and *Pantoea* ($p = 0.042$) treated plants have

a significantly higher median root width than the open pollinated plants do when compared independently. All comparisons were conducted using Kruskal Wallis tests.

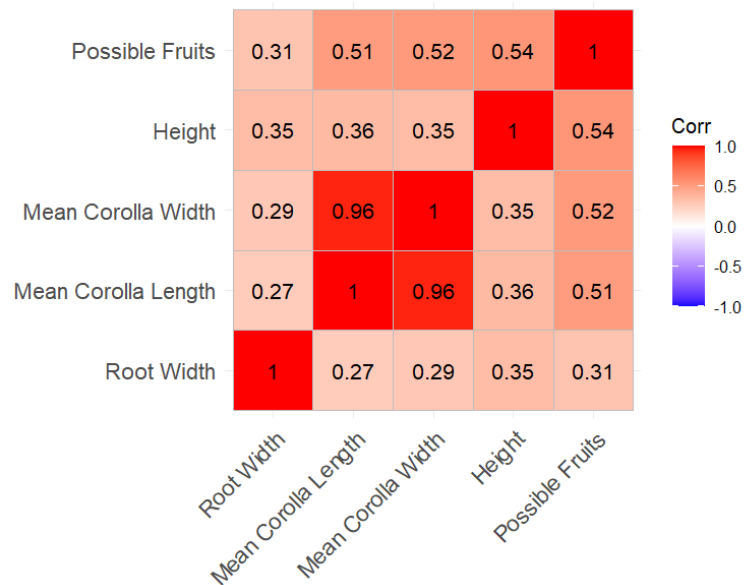


Figure 2. Correlation heat map showing correlation between root width, average corolla length, average corolla width, height, and possible fruits of all plants. All variables are tested independently.

There was very high correlation amount all measures of plant traits taken. We found an almost perfect correlation between average corolla length and average width. We used these 2 corolla measurements to make a PCA of flower size to determine flower size's effect on fitness. Height and root width were also chosen than also made into a PCA to determine the effect of plant traits on treatment.

Trait	PC1 (Flowers)	PC2 (Flowers)	PC1 (Traits)	PC2 (Traits)
Corolla Length (ave_corL)	-0.707	0.707		
Corolla Width (ave_corW)	-0.707	-0.707		
Height			-0.707	-0.707
Root Width			-0.707	0.707

Table 1. a) Principal components analysis results for floral traits. b) Principal components analysis results for plant traits

The principal components analysis for both floral and plant traits for PC1 were weighted negatively. When plotted, as the x-axis decreases it represents the flowers or plant traits increasing in size

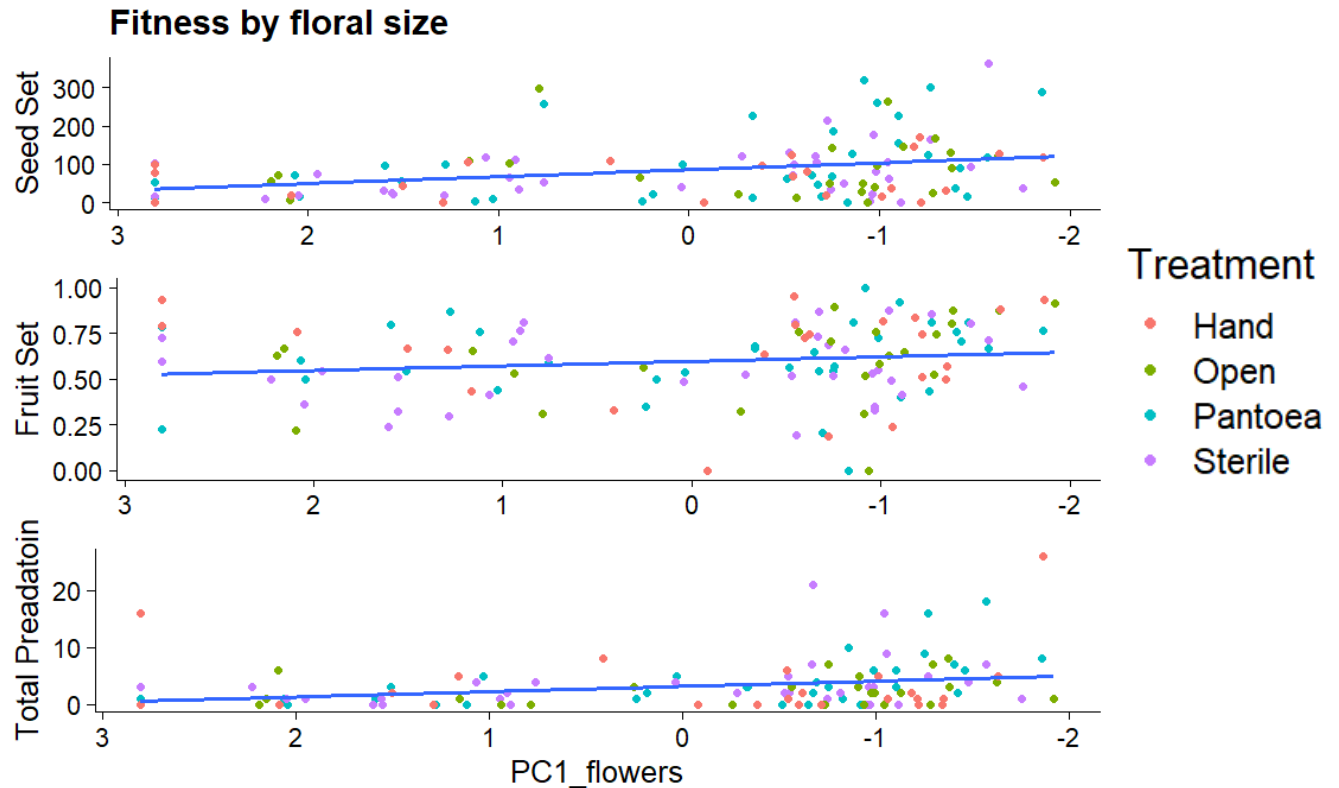


Figure 3.

Relationships between floral size (PC1_flowers) and three fitness-related measures:

- a) Seed set ($p = 0.0013$),
- b) Fruit set ($p = 0.131$),
- c) Total predation ($p < 0.02$).

Principal components analysis (PC1_flowers) of floral traits is scaled negatively, such that larger floral size corresponds to more negative values. For interpretability, the x-axis has been reversed. Both seed set and total predation were significantly associated with larger flowers, while fruit set showed a nonsignificant positive trend. Treatment had no significant effect on any of these relationships.

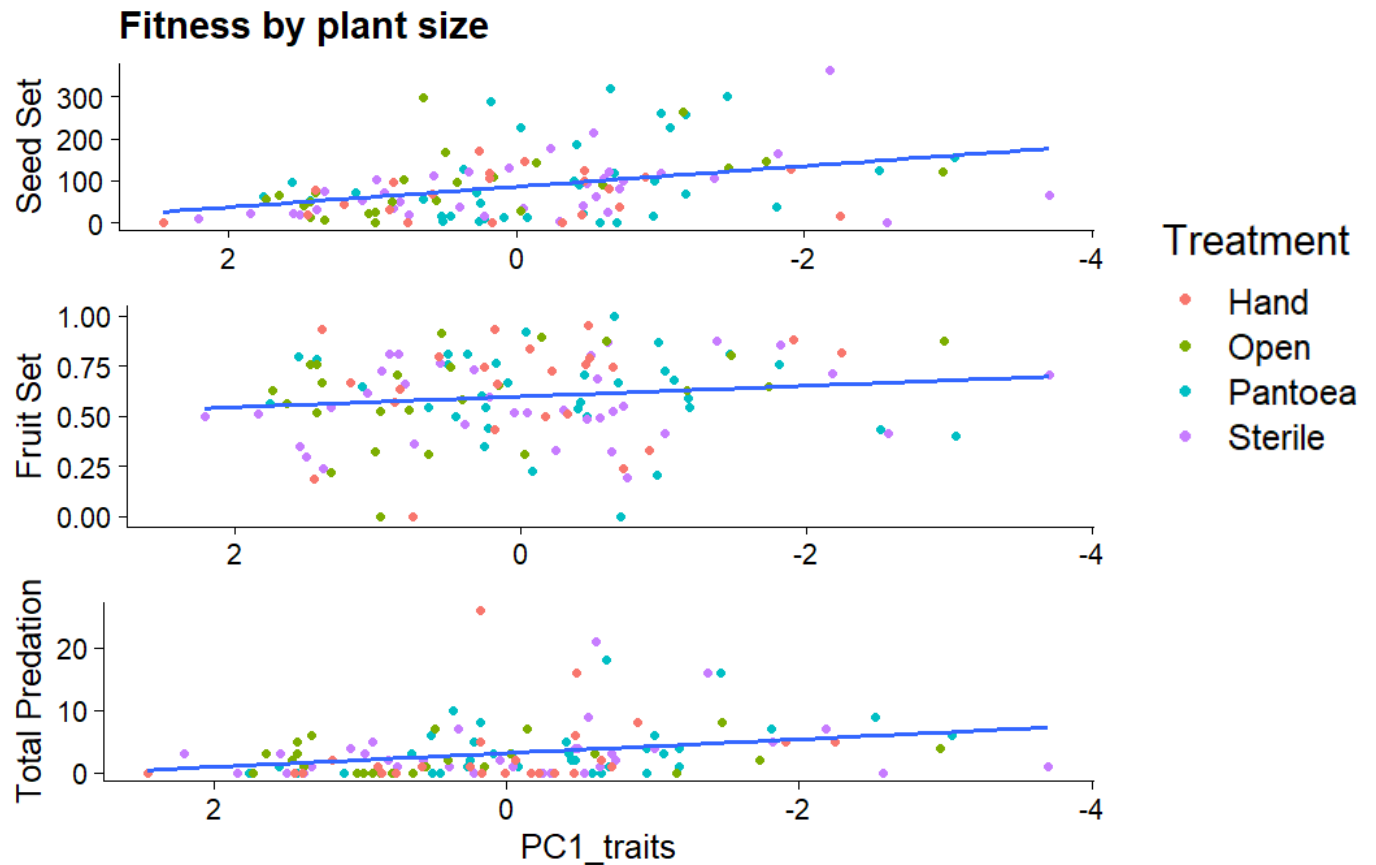


Figure 4.

Relationships between plant size (PC1_traits) and three fitness measures:

- a) Seed set ($p = 3.37e-05$),
- b) Fruit set ($p = 0.122$),
- c) Total predation ($p = 0.0001$).

Principal components analysis (PC1_traits) for plant traits is scaled negatively, such that larger plant size corresponds to more negative values. Seed set and total predation both show significant negative associations with plant size, while fruit set shows a nonsignificant positive trend. Treatment groups had no significant effect on any of these relationships. The x-axis was reversed for easier interpretation.

Fitness Metric	Pollen Limitation Value	Interpretation
Fruit Set	0.055	Hand pollination resulted in a 5.5% increase in fruit set compared to open pollination (weak pollen limitation).
Seed Set	-0.321	Hand pollination resulted in a 32% decrease in seed set compared to open pollination (no pollen limitation, possible cost).

Table 2. Pollen limitation results for seed set and fruit set. (Hand vs Open Pollinated treatments).

Positive values indicate pollen limitation, and negative values represent no limitation.

Our pollen limitation value for fruit set (Average hand pollinated fruit set / average open pollinated fruit set) is 0.055 or 5.5%. Our pollen limitation value for seed set (Average hand pollinated seed set / average open pollinated seed set) is -0.32 or -32%. Hand pollination produced 5.5% more fruits but 32% less seeds than our open pollination treatment. There is also no significant difference between seed set, fruit set, or total predation for hand or open pollinated treatments.

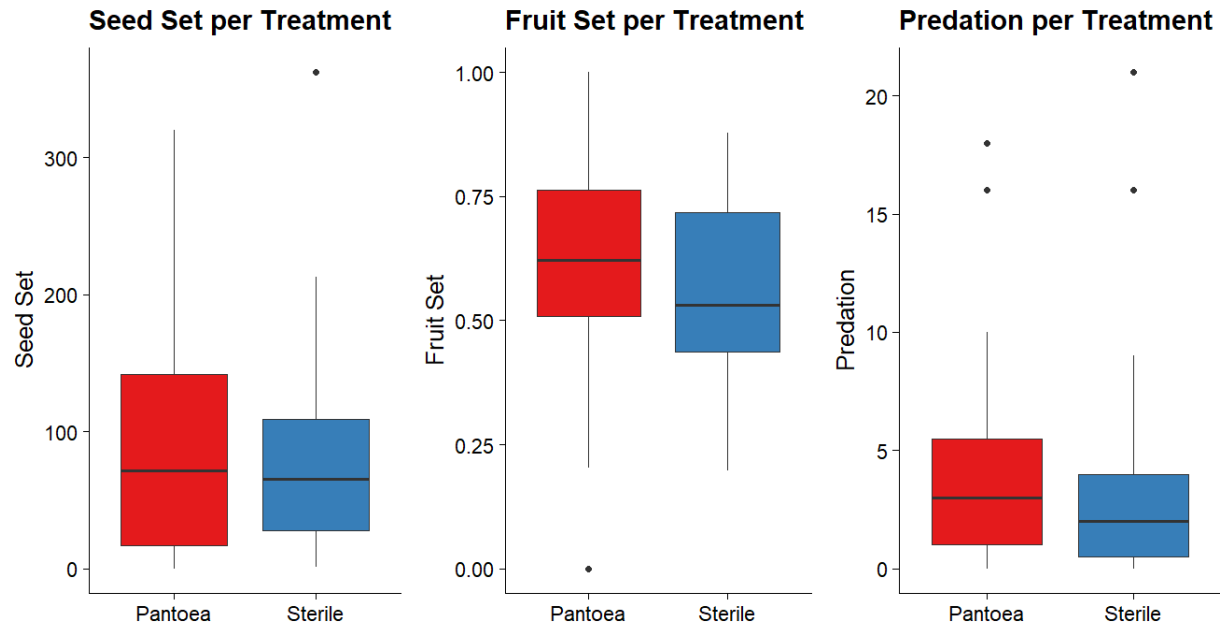


Figure 5. Fitness Measurements per inoculation treatment

a) Seed set per treatment ($p = 0.7601$, $w = 639$).

b) Fruit set per treatment ($p = 0.2324$, $w = 695$).

c) Total predation per treatment ($p = 0.5248$, $w = 666.5$).

No significant differences were found in any fitness metric between the Pantoea and Sterile inoculation treatments. All comparisons were conducted using Wilcoxon rank-sum tests.

Discussion

Traits Effects on Female Fitness

When we analyzed trait distribution across treatment groups, we found that root width was significantly larger in hand-pollinated and Pantoea-treated plants compared to open-pollinated plants. This result was concerning, as it suggests that the initial random assignment of plants to

treatments may have introduced trait-based bias, which could affect pollination outcomes (cite). All other measured traits — height, average corolla length, and average corolla width — did not differ significantly among treatments. In our principal component analysis of floral traits (PC1_flowers), we found a significant positive association between floral size and both seed set and fly larvae predation. Similar patterns were observed when analyzing plant size using PC1_traits. Fruit set, however, was not significantly associated with either floral or plant size. Treatment and inoculation effects were included in all models but showed no significant interaction with plant or floral size on fitness outcomes. To further explore whether pollination was limiting reproduction, we compared seed set and fruit set between our hand and open pollinated treatments. Hand pollination produced 5.5% more fruits than open pollination, indicating only weak pollen limitation for fruit set. Surprisingly, seed set was 32% lower in hand-pollinated plants than in open-pollinated ones, suggesting no pollen limitation. The decrease in seed set suggests that hand pollination could be costly for *Ipomopsis aggregata*. These results align with our model outputs, which showed no significant differences in any fitness measures (seed set, fruit set, or predation) between hand and open treatments, and support the conclusion that natural pollination was sufficient in this system.

These findings suggest that *Ipomopsis aggregata* individuals with larger floral displays and overall plant size are more attractive to pollinators, likely hummingbirds, and therefore exhibit higher seed set. However, this increased visibility may also attract more florivorous fly larvae, indicating a potential ecological trade-off between pollination and predation.

Pantoea Inoculated Nectar Effects on Female Fitness

We found no significant effect of *Pantoea*-nectar on any female fitness measure. This result does not support our hypothesis that bacterial nectar would deter hummingbirds and reduce fitness in

Ipomopsis aggregata. Seed set, fruit set, and predation did not differ significantly between the *Pantoea* treatment and any other inoculation group. Interestingly, *Pantoea*-treated and sterile nectar treatments produced nearly identical outcomes, suggesting that the presence of *Pantoea* sp. did not alter hummingbird behavior under field conditions.

These results contrast with previous research suggesting microbial nectar can disrupt pollinator visitation (Vannette et al., 2013), including behavioral studies involving *Selasphorus platycercus* (cite). Previous research has shown that nectar-inhabiting microbes can alter nectar chemistry and reduce pollinator visitation (e.g., Vannette & Fukami 2016). However, such effects may be pollinator-specific. Hummingbirds, for example, may be less sensitive to microbial alterations in nectar than bees, due to differences in foraging behavior and sensory ecology (Ernest et al., 2024). This could explain why *Pantoea* inoculation had no measurable impact on fitness in our study. A key distinction is that past studies often used nectar-specialist microbes in artificial systems, whereas we used a plant-generalist bacterium in a natural field setting. These discrepancies imply that the role of nectar-inhabiting microbes in shaping plant–pollinator interactions may be more context-dependent than previously understood — influenced by microbial strain, nectar chemistry, and the identity of the plant or pollinator involved

Implications for microbial mediation of pollination

These results have two suggestions: 1) The field- realistic concentration of *Pantoea* sp. used was too subtle to elicit behavioral response in Hummingbirds, or 2) Hummingbirds are not deterred by certain bacterial species. Previous work (Scheiner et al., 2020) demonstrated that higher concentrations of *Pantoea* sp. in nectar reduced foraging by *Apis mellifera*. It's possible that

increasing the microbial load in our system would have affected pollinator behavior and reduced female fitness, but we prioritized ecological realism over artificial effect strength.

While microbial nectar has previously been shown to reduce individual plant fitness, and Hummingbird attractiveness in lab-based studies (Vannette et al., 2013), our findings suggest that not all nectar-inhabiting bacteria disrupt plant–pollinator mutualisms, particularly under natural field conditions. This highlights the importance of context in microbial mediation of plant–pollinator interactions. While bacterial nectar previously been shown has been shown to decrease individual plant fitness, our results suggest that not all nectar-inhabiting bacteria disrupt plant–pollinator mutualisms, particularly under realistic field conditions.

Conclusion

My data shows that plant morphology alone can influence the fitness of *Ipomopsis aggregata* by way of varied seed set and predation. Taller plants and those with larger floral displays are more likely to attract pollinators, resulting in higher seed set, but also more likely to experience increased larval predation, suggesting an ecological trade-off. This suggests that there may be a ecological tradeoff between bigger and more elevated floral displays for pollinators and for predators. In contrast, the epiphytic bacterium *Pantoea* sp. did not significantly influence any measured fitness traits. Both *Pantoea* and sterile nectar treatments resulted in similar levels of pollination and seed production, suggesting that inoculation with this generalist bacterium does not interfere with plant reproductive success in this system.

The observed variation in root width across treatments, particularly its inclusion in the plant size PCA, may have contributed unintended bias in the trait–fitness relationships. While our models accounted for treatment, it remains possible that underlying trait variation affected the results.

Nonetheless, we found no treatment effects on fitness overall, reinforcing the conclusion that plant traits, not nectar microbiota, played a dominant role in shaping fitness outcomes in this study.

References:

- Abrahamczyk, S., Weigend, M., Becker, K., Dannenberg, L. S., Eberz, J., Atella-Hödtke, N., & Steudel, B. (2025). *Data from: Influence of plant reproductive systems on the evolution of hummingbird pollination* (Version 8, p. 39363 bytes) [Dataset]. Dryad.
<https://doi.org/10.5061/DRYAD.BNZS7H4CJ>
- Campbell, D. R., Waser, N. M., Price, M. V., Lynch, E. A., & Mitchell, R. J. (1991). COMPONENTS OF PHENOTYPIC SELECTION: POLLEN EXPORT AND FLOWER COROLLA WIDTH IN *IPOMOPSIS AGGREGATA*. *Evolution*, 45(6), 1458–1467.
<https://doi.org/10.1111/j.1558-5646.1991.tb02648.x>
- Ernest, H. B., Tell, L. A., Bishop, C. A., González, A. M., & Lumsdaine, E. R. (2024). Illuminating the Mysteries of the Smallest Birds: Hummingbird Population Health, Disease Ecology, and Genomics. *Annual Review of Animal Biosciences*, 12(1), 161–185.
<https://doi.org/10.1146/annurev-animal-021022-044308>
- Irwin, R. E. (2000). Hummingbird avoidance of nectar-robbed plants: Spatial location or visual cues. *Oikos*, 91(3), 499–506. <https://doi.org/10.1034/j.1600-0706.2000.910311.x>
- Irwin, R. E., & Brody, A. K. (1998). *Nectar robbing in Ipomopsis aggregata: Effects on pollinator behavior and plant fitness*.
- Irwin, R. E., Bronstein, J. L., Manson, J. S., & Richardson, L. (2010). Nectar Robbing: Ecological and Evolutionary Perspectives. *Annual Review of Ecology, Evolution, and Systematics*, 41(1), 271–292. <https://doi.org/10.1146/annurev.ecolsys.110308.120330>
- Kim, A. Y., Rankin, D. T., & Rankin, E. E. W. (2021). What is that smell? Hummingbirds avoid foraging on resources with defensive insect compounds. *Behavioral Ecology and Sociobiology*, 75(9), 132. <https://doi.org/10.1007/s00265-021-03067-4>

- McGrady, C. M., Troyer, R., & Fleischer, S. J. (2020). Wild Bee Visitation Rates Exceed Pollination Thresholds in Commercial *Cucurbita* Agroecosystems. *Journal of Economic Entomology*, 113(2), 562–574. <https://doi.org/10.1093/jee/toz295>
- Morin, A. (2014). Pantoea. In *Encyclopedia of Food Microbiology* (pp. 1028–1032). Elsevier. <https://doi.org/10.1016/B978-0-12-384730-0.00245-7>
- Morris, M. M., Frixione, N. J., Burkert, A. C., Dinsdale, E. A., & Vannette, R. L. (2020). Microbial abundance, composition, and function in nectar are shaped by flower visitor identity. *FEMS Microbiology Ecology*, 96(3), fiae003. <https://doi.org/10.1093/femsec/fiae003>
- Núñez, P., Méndez, M., & López-Rull, I. (2021). Can Foraging Hummingbirds Use Smell? A Test with the Amazilia Hummingbird *Amazilia amazilia*. *Ardeola*, 68(2). <https://doi.org/10.13157/arla.68.2.2021.sc2>
- O'Connor, E. (2017). *Hummingbird Foraging Preference: The Hierarchical Impacts of Color, Position, and Concentration on Visitation Frequency*.
- Otieno, B. A. (2020). The Role of Pollinators in Plant Reproduction: Their Ecological Interactions, Evolutionary Adaptations, and the Impact on Biodiversity Conservation. *Australian Herbal Insight*, 3(1), 1–5. <https://doi.org/10.25163/ahi.319923>
- Palmer, T. M., Doak, D. F., Stanton, M. L., Bronstein, J. L., Kiers, E. T., Young, T. P., Goheen, J. R., & Pringle, R. M. (2010). Synergy of multiple partners, including freeloaders, increases host fitness in a multispecies mutualism. *Proceedings of the National Academy of Sciences*, 107(40), 17234–17239. <https://doi.org/10.1073/pnas.1006872107>

- Rankin, D. T., Clark, C. J., & Wilson Rankin, E. E. (2018). Hummingbirds use taste and touch to discriminate against nectar resources that contain Argentine ants. *Behavioral Ecology and Sociobiology*, 72(3), 44. <https://doi.org/10.1007/s00265-018-2456-z>
- Scheiner, R., Strauß, S., Thamm, M., Farré-Armengol, G., & Junker, R. R. (2020). The Bacterium *Pantoea ananatis* Modifies Behavioral Responses to Sugar Solutions in Honeybees. *Insects*, 11(10), 692. <https://doi.org/10.3390/insects11100692>
- Tilley, D.-N., & Aberdeen, I. (2017). *Plant Guide for scarlet gilia (Ipomopsis aggregata)*.
- Vannette, R. L., Gauthier, M.-P. L., & Fukami, T. (2013). Nectar bacteria, but not yeast, weaken a plant–pollinator mutualism. *Proceedings of the Royal Society B: Biological Sciences*, 280(1752), 20122601. <https://doi.org/10.1098/rspb.2012.2601>