

**Comparing pollen distribution on pollinators to floral community composition in the East
River Valley**

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Abstract

While plant-pollinator networks are salient markers of biodiversity, their mechanisms remain poorly understood. One theory describing pollination interactions is the Neutral Theory of Biodiversity, which asserts that plant-pollinator interactions are neutral, random processes based on species' abundances. Other theories emphasize the importance of niches and species' identities and traits in the pollination process. This study explores whether plant-pollinator interactions over June and July 2021 across two sites in the East River Valley, CO, are neutral or non-neutral by comparing the pollen diversity on solitary bees to that of the local floral community. Solitary bees were caught in transects and vortexed in the lab to obtain their collected pollen. Pollen slides were made from the collected pollen, and the pollen was counted and identified under a microscope. From a two-sample t-test and a generalized linear mixed effects model run in R, the pollen diversity on the solitary bees was found to be significantly different from the floral community diversity, indicating non-neutral interactions and implying potential solitary bee preferences for flowers with larger display sizes, shorter flower height, and wider corolla widths. Flower color is another possible contributor to bee preference; however, further studies directly comparing different flower colors are needed. Future studies examining the connection between the floral traits and floral rewards could reveal important plant-pollinator network mechanisms.

Introduction

Background

Ecological communities center around interspecific interactions. Patterns of such interactions can be represented in networks that are mutualistic (+/+) or antagonistic (+/-) (Tylianakis et al., 2010). For example, plant-pollinator interactions are mutualistic—the plant benefits as the pollinator aids its reproduction via pollen transfer, and the pollinator benefits from nutritional resources—while predator-prey interactions are antagonistic—the predator benefits by consuming the prey, but the prey is harmed (Tylianakis et al., 2010). These networks describe the relationships between species in natural communities and reflect biodiversity.

Plant-pollinator networks are integral in supporting ecosystem biodiversity and food crops (Burkle et al., 2013). Almost 90 percent of angiosperms and 75 percent of global food crops depend on animal pollinators (Klein et al., 2007). It is important to protect these networks, both the floral communities and the pollinators, as greater diversity in one contributes to greater diversity in the other (Bluthgen and Klein, 2011), which then sustains the ecosystems and trophic levels that rely on their interactions. However, the ecological and evolutionary processes shaping the structural patterns of mutualistic networks like plant-pollinator networks are still poorly understood (De Andreazzi et al., 2020). By learning how these networks function, we will gain a broader understanding of the species involved and their interactions so that we may predict how

they change in the future. We could better understand how our actions impact these networks and how we can protect and preserve them.

For ecological networks, neutrality has been proposed as a possible explanation for observed mutualistic patterns (Vasquez, 2005). Specifically, the Neutral Theory of Biodiversity (NTB) asserts that observed mutualistic patterns result from differences in species abundances (Coelho and Rangel, 2018). For example, if plant-pollinator networks were neutral processes, then we would observe any pollinator randomly pollinating plants it bumps into. Pollinators would not consider the species, traits, or competitive dynamics of the pollinator or plant.

In contrast to NTB, deterministic processes are patterns driven by niches—by species identities and traits, accounting for ecological value and competitive dynamics (Chase and Myers, 2011). Deterministic processes are non-neutral and focus on inherent differences to explain species diversity and composition (Chase and Myers, 2011). For example, if plant-pollinator networks were deterministic processes, then we would observe specific pollinators pollinating specific plants, and pollination would depend on the differences between pollinators and between plants, such as longer tongues or flower color.

Currently, it is still inconclusive whether plant-pollinator interactions are neutral or non-neutral. While there is empirical evidence of more pollinators visiting plant species with larger flowers, it is still unknown what influences pollinators in general to visit or not visit certain species over others (Lazaro et al., 2013). Yet, the implications of either process accurately describing the network are fascinating. If plant-pollinator networks are neutral, that would imply that floral abundance is more salient in successful pollination than the floral species and their unique traits. This might also imply that flower species that have evolved to reproduce more abundantly will be more successful.

Alternatively, if plant-pollinator networks are deterministic, that would imply that pollinators have some preference for particular flowers based on qualities like nutrient needs, or that specific floral traits are more successful in attracting pollinators than others like through color or display size. In this case, floral abundance would not be as important as the different floral species, and pollinators would collect pollen or nectar from favored flowers.

Hypothesis

I hypothesized that the composition of pollen collected by bees would differ from that of the floral community. Because there is evidence of some pollinators visiting plants with larger flowers or blue-colored flowers more often, I predicted that bees would preferentially visit flowers with specific traits or more attractive floral rewards (Giurfa et al., 1995; Lazaro et al., 2013). If bees visited certain flowers over others, then the pollen diversity on bees would differ

from the floral diversity. To test this prediction, bees were caught in various transects, and the distribution of their collected pollen was analyzed and compared to the floral community composition at the catch site.

Methods

This observational study was conducted at two meadows near Gothic, Colorado—Rustlers Gulch and Stupid Falls (Figure 1). At each site, three one-by-ten meter transects with segments taped off every two meters were set up. Each site was sampled three times, one day per week, during June and July of 2021. Sampling rounds began around 10:00 am, 12:00 pm, and 2:00 pm and consisted of catching bees in vials containing ethyl acetate. Bees were only caught if they landed on the reproductive parts of flowers in the transects, indicating that they were actively pollinating. However, due to excessive historic sampling of bumblebees in the RMBL area, we did not collect bumblebees in this study.

The transect segments were randomly sampled to avoid bias, and each segment was observed for pollinators for 1.5 minutes on each side. Wind speed, relative humidity, soil moisture, and floral counts at each site were recorded as well. The traits (color, height, flower display size, corolla depth and width, and stigma height) of floral species found within the transects were also recorded for later analysis of potential pollinator preferences.

In the lab, the bees were transferred into microcentrifuge tubes labelled with specimen numbers. After adding 1000 μ l of soapy water to those tubes, the bees were vortexed for around 30 seconds, or until most of the pollen was shaken from the pollinators. The bees were then transferred to new microcentrifuge tubes labelled with specimen numbers corresponding to those on the first batch of tubes, so the specific pollen collected by each bee was known. While the pollinator tubes were filled with 95 percent ethanol and set aside, the first batch of tubes with the soapy water and pollen were centrifuged to obtain pollen pellets. The soapy water was pipetted out, and 200 μ l of ethanol was added to prevent the pollen from germinating.

To prepare the pollen slides, the microcentrifuge tubes containing the bee pollen were vortexed for around ten seconds to resuspend the pollen. Next, 10 μ l of the pollen ethanol solution was pipetted onto a microscope slide. After the ethanol dried, a 2 mm³ cube of fusion gel was cut and placed atop the pollen on the slide. The gel was heated until the cube just started to melt. When the gel finished melting completely, a cover slide was placed over the melted gel, and then spreading clear nail polish along the edges, the cover slide was sealed to the microscope slide. Each slide was taped and labelled with the specimen number, site where the pollen was collected, and the date the pollen was collected.

Using a compound microscope, the pollen from each slide was counted. Two-by-two grid boxes were drawn on a cover slide, and the cover slide was placed over the pollen slides. The first one hundred pollen grains on each slide were counted, starting from the top left grid box and moving to the right and then dropping down to the next row and moving right again. Pictures of the pollen were taken at 40X and 100X magnification, and from the pictures, the different types of pollen were identified using two pollen reference libraries and reference slides made with pollen from Rustlers Gulch and Stupid Falls.

With the statistical program R, the distribution of pollen types and the pollen diversity were compared to the distribution and diversity of the floral community at Rustlers Gulch and Stupid Falls. Specifically, the richness, relative abundance, and total abundance of the pollen types were compared to those of the floral community to obtain a Shannon diversity metric of the pollen and floral community. Boxplots of the diversities were generated with the pollen and floral diversities on the x-axis and the diversity metrics on the y-axis. A Welch two-sample t-test was performed for significant difference between the pollen and floral diversities. Finally, to investigate what plant traits might drive the difference in pollen and plant diversities, a generalized linear mixed effects model was run to determine the impact of various floral traits on bee foraging habits. The floral traits chosen were color, average stigma length, average corolla depth, average corolla width, average flower height, and average display size. Previous studies have found that color, corolla size, flower height, and display may contribute to pollinator preferences by attracting pollinators in different ways. Stigma length may be related to floral rewards and pollination frequency. The floral traits with significant impact were then graphed to illustrate the direction of impact on bee visitation.

Results

Diversity Metrics

Using R, the Shannon diversity metrics were calculated for the pollen and plant community compositions. After running a Welch two-sample t-test to compare the pollen and plant community diversities, it was found that the pollen and plant diversities were significantly different, with a p-value of $3.927e^{-15}$. Greater Shannon diversity metrics indicate a more diverse and equally distributed community, while lower diversity metrics indicate a less diverse and unequally distributed community. The pollen collected from bees was less diverse than and not as equally distributed as the floral community, as seen from Figure 2 where the pollen diversity is notably lower than the plant community diversity.

Floral Trait Impacts on Difference in Diversity

From the generalized linear mixed effects model, the blue/dark purple and orange/yellow colors, average corolla width, average display size, and average flower height significantly impact the observed difference in pollen and plant diversities (Table 1). To analyze the effect of flower color

more generally, an ANOVA was performed that confirmed the significance of average corolla width, average display size, and average flower height and emphasized the significant contribution of flower color to the difference in pollen and plant diversities (Table 2).

To investigate the direction of impact, the floral traits were graphed with the magnitude of difference between the pollen and plant diversities on the y-axis and the various floral traits on the x-axis (Figures 3-6). For Figures 2-6, the blue trend line illustrates the positive effect of the floral trait on the difference between pollen and plant diversities in the form of increased pollinator visitation, while the red trend line illustrates the negative effect of the floral trait on the difference between pollen and plant diversities in the form of decreased pollinator visitation.

Discussion

Pollen vs. Plant Diversity

From the pollen and floral community compositions, the plant-pollinator interactions across Stupid Falls and Rustlers Gulch seem non-neutral and appear to be driven by various floral traits. As shown in Figure 1, the Shannon diversity metric for the pollen appears different from that for the plant community. This observation is corroborated by the p-value of $3.927e^{-15}$ obtained from the Welch two-sample t-test, indicating that the difference in diversities between the pollen and plant community is statistically significant and that there is a true difference. These results support my hypothesis that the pollen composition on bees differs from the floral community composition and that these interspecific interactions are non-neutral. Notably, the pollen diversity is significantly lower than the plant diversity, as Figure 1 illustrates. Since the bees only visited certain flowers—not all floral species in the plots—it is reasonable that the pollen diversity was lower. Because the pollen and floral community diversities differ, this shows that solitary bees at Stupid Falls and Rustlers Gulch collected pollen from certain flowers more than others, possibly implying that solitary bees prefer certain floral species to others.

P-values and Drivers of Plant-Pollinator Interactions

Exploring the concept of pollinator preferences, from Table 1 it appears that the floral traits of color (specifically blue/dark purple and orange/yellow), display size, average corolla width, average flower height, and average display size significantly contribute to the difference in pollen and floral diversity—also contributing to the difference in solitary bee visitation among the floral species. The ANOVA results in Table 2 also support that the aforementioned traits significantly influence bee visitation. The impacts of average stigma length and average corolla depth do not appear to be statistically significant.

Average Corolla Width

Examining Figure 2, the blue trend line illustrates how average corolla width has a large positive effect on the difference in pollen and plant diversities, while the red trend line illustrates how corolla width has a small negative effect. The magnitude of difference between the pollen and plant diversities shown on the y-axis can be interpreted as the bee visitation frequency if it is assumed that more pollen indicates that the bee visited that flower more often. Thus, as the average corolla width increases, so does solitary bee visitation frequency, whereas the red trend line is fairly flat, indicating that the lack of bee visitation is not impacted by corolla width. These results imply that solitary bees tend to visit or prefer flowers with wider corollas.

Another study has shown that other pollinators, such as bats, also tend to visit flowers with wider corollas more often than they will flowers with narrower corollas (Muchhala, 2007). This pattern is thought to be related to floral rewards, in which when the bat's snout better fits the corolla, the bat will obtain more nectar (Muchhala, 2007). Thus, perhaps the reason why solitary bees prefer flowers with wider corollas is also connected to complementary corollas and gaining greater floral rewards.

Average Flower Height

For Figure 3, the blue trend line shows how average flower height has a large effect on bee visitation. Specifically, as the average height of flowers increases, the solitary bee visitation decreases, indicating that perhaps solitary bees tend to forage closer to the ground. The red trend line supports this conjecture, as the average height increases, so does the lack of visitations.

In contrast, previous studies have found that pollinators seem to prefer taller flowers (Lortie and Aarssen, 1999; Sletvold et al., 2010; Zu and Schiestl, 2017). Specifically, bumble bees were observed visiting taller *Dactylorhiza lapponica* and *Brassica rapa* more frequently than their shorter counterparts, perhaps because taller flowers are thought to draw attention away from other flowers, thereby attracting more pollinators (Aarssen, 1995; Sletvold et al., 2010; Zu and Schiestl, 2017). Therefore, the conflicting results from our study may arise from a difference in bumble bee and solitary bee foraging heights, since the solitary bee would not notice the taller flowers as often if it flies beneath them.

Average Floral Display Size

Concerning Figure 4, the blue trend line illustrates how average display size has a large positive effect on bee visitation, whereas the red line depicts a negative effect. As average display size increases, so does the visitation frequency, while the lack of visitation decreases simultaneously, implying that solitary bees favor flowers with larger display sizes.

In previous studies, pollinators have also exhibited a preference for larger floral displays (Mitchell et al., 2004; Parra-Tabla and Vargas, 2007). Particularly, bumble bees have been shown to visit *Mimulus ringens* flowers with larger floral displays more often, thought to occur because larger displays decrease the likelihood the bee will revisit that flower, which increases the floral reward for the pollinator (Mitchell et al., 2004). Another study also concluded that larger floral display sizes in *Myrmecophila christinae* increased pollination success (Parra-Tabla and Vargas, 2007). However, it is still unclear whether the higher visitation frequency is due to the larger display being easier to detect (Mitchell et al., 2004). Concerning our study, perhaps solitary bees also favor larger displays because they are easier to detect or have learned to associate the larger display with greater floral rewards.

Flower Color

Finally, with Figure 5 there appears to be a large spread of positive and negative impacts on bee visitation. Blue/dark purple and orange/yellow have a wide range of impact, with both negative and positive spreads, which makes it difficult to determine if those colors result in higher or lower visitation frequencies. However, pink/light purple has a small negative impact, while white has a small positive impact, so perhaps solitary bees do tend to prefer pink/light purple flowers yet do not prefer white flowers—though this cannot be concluded since the visitation frequencies for the different colors were not tested against each other.

The correlation between flower color and pollinator preferences is still poorly understood. However, some studies have shown that syrphid flies prefer yellow over white flowers, while solitary bees prefer white over yellow flowers (Campbell et al., 2010). Other studies have explored the idea that pollinators associate floral rewards with color after foraging and learn that certain colors correspond to certain floral rewards (Gumbert, 2000; Dyer and Murphy, 2013). While our study does not support that solitary bees prefer white flowers, it does support that flower color significantly influences pollinator visitation. Perhaps different species of solitary bees associate greater floral rewards with different flower colors, resulting in the wide spread of pollinator visitation frequencies seen in Figure 5.

Stigma Length and Average Corolla Depth

From Tables 1 and 2, the impacts of average stigma length and average corolla depth on the difference between pollen and plant diversity do not appear to be statistically significant. Regarding stigma length, it could be that the length of the stigma does not affect floral rewards, nor does it facilitate pollination frequency or attract solitary bees, especially if the bees are searching for nectar and pollen only. For corolla depth, interestingly most studies seem to focus on corolla shape and size, not just corolla depth or corolla width alone (Conner and Rush, 1996; Muchhala, 2007; Kaczorowski et al., 2012). These studies have demonstrated that corolla shape

and size are important for pollination success and attracting specific pollinators. Thus, it was odd that corolla width was significant while corolla depth was not, since depth is a component of corolla shape and size and floral rewards. For future studies, it might be beneficial to trait more individuals of relevant floral species to obtain a larger, more representative sample size to see if corolla depth is indeed significant.

Error Analysis of Methods

When looking at the pollen slides, some bees appeared to only have one type of pollen. Perhaps for these bees, they were caught when they just started foraging—when they had only visited one flower. In this case, only one interaction was represented in the pollen, not multiple. Thus, it is unknown whether that species of solitary bee usually visits just that one flower species—indicating non-neutral processes—or if the bee forages randomly—indicating neutral interactions—which would skew the diversity metrics. Another challenge was identifying the pollen on the slides, as some pollen types look very similar to each other. An additional study could entail confirming the pollen identification via metabarcoding.

Conclusion

Much is still unknown regarding plant-pollinator interactions and what dictates observed pollination networks. At Stupid Falls and Rustlers Gulch, bee-plant interactions seem to be non-neutral processes, implying possible pollinator preferences or specializations. From the generalized linear mixed effects model, wider corollas, shorter flower height, and larger display size significantly drive solitary bee visitation frequency. However, while flower color also appears to significantly impact bee visitation, it is still unclear which colors better attract solitary bees. Further studies are necessary to investigate the floral trait trends, especially with regard to color, corolla width, and height. Previous studies have demonstrated that these three traits could be indicators of floral rewards. For future studies, examining pollinator preferences through floral rewards may reveal more about the mechanisms of plant-pollinator interactions so that we may better understand and protect the systems and lives that depend on them.

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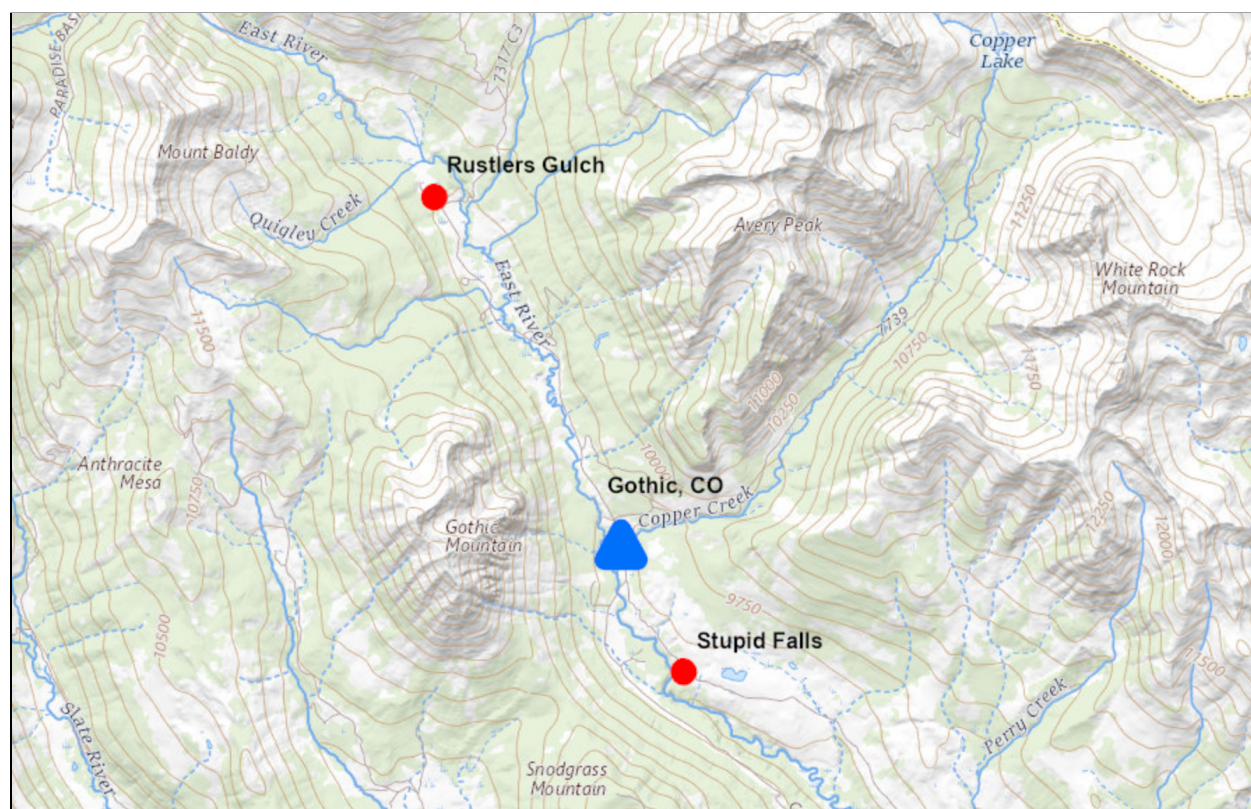
Figures and Tables

Figure 1. Map of research sites and Gothic, CO. The two research sites—Stupid Falls and Rustlers Gulch—are shown in red. The Gothic townsite is shown in blue.

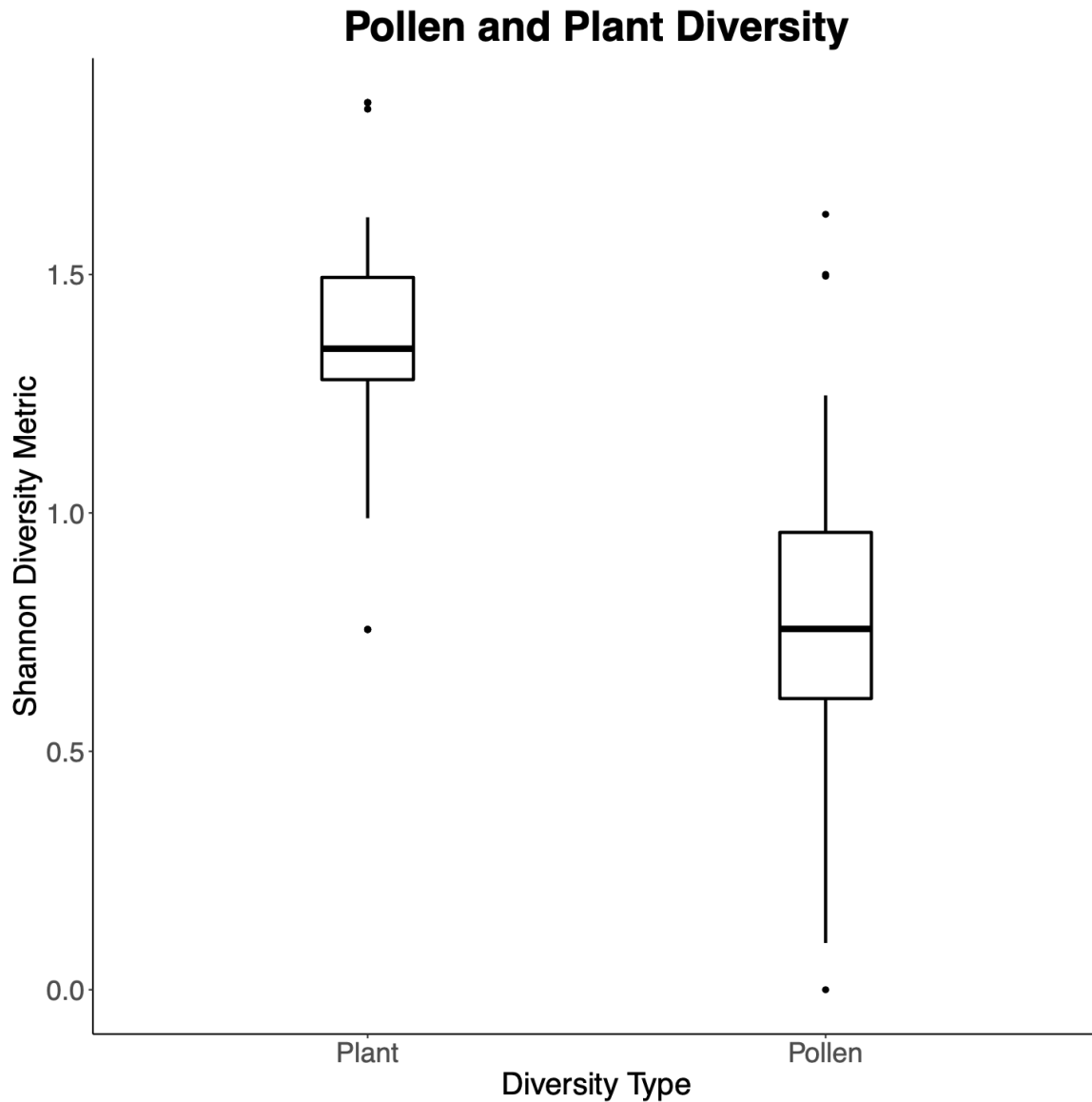


Figure 2. Boxplots of the pollen and plant community diversities. The diversities are significantly different with a p-value of $3.927e^{-15}$. The pollen diversity metric is significantly lower than the plant community diversity metric.

Table 1. P-values from Generalized Linear Mixed Effects Model

All traits except for pink/light purple, white, average stigma length, and average corolla depth significantly impact the observed difference in pollen and plant diversities.

Floral Trait	P-value
Color - blue/dark purple	0.00231 **
Color - orange/yellow	0.000563 ***
Color - pink/light purple	0.132
Color - white	0.181
Average stigma length	0.822
Average corolla depth	0.199
Average corolla width	0.000352 ***
Average flower height	0.0131 *
Average display size	0.0288 *

Codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 2. P-values from ANOVA

All traits except average stigma length and average corolla depth significantly impact the observed difference in pollen and plant diversities. Note that all p-values except for color match those in Table 1. Color in general is significant.

Floral Trait	P-value
Color	0.0000655 *****
Average stigma length	0.822
Average corolla depth	0.199
Average corolla width	0.000352 ***
Average flower height	0.0131 *
Average display size	0.0288 *

Codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ***** $p < 0.0001$

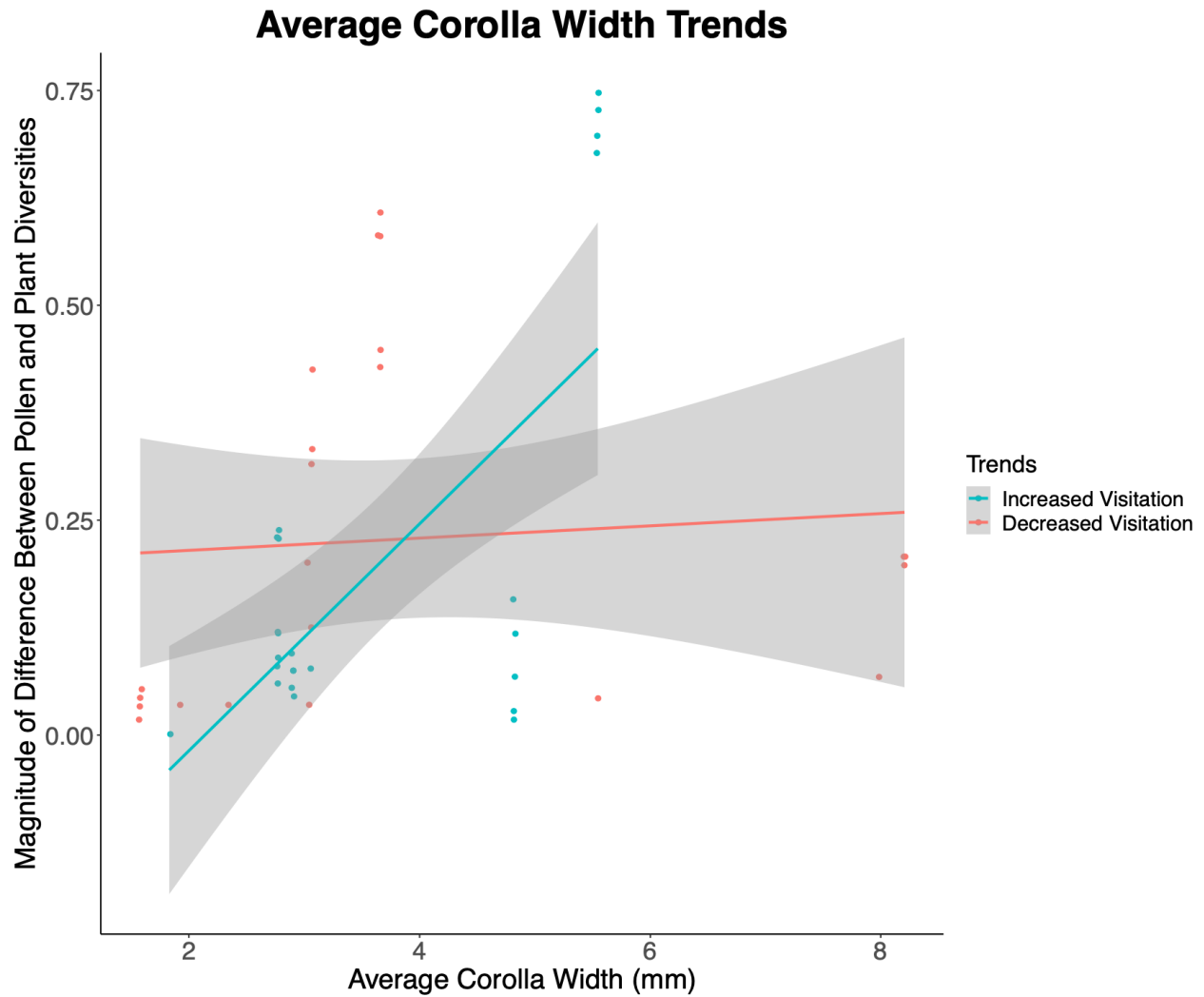


Figure 3. The blue trend line illustrates how average corolla width has a large positive effect on the difference in pollen and plant diversities, while the red trend line illustrates how corolla width has a small negative effect. The blue line indicates increased pollinator visitation frequency, and the red line indicates decreased pollinator visitation frequency.

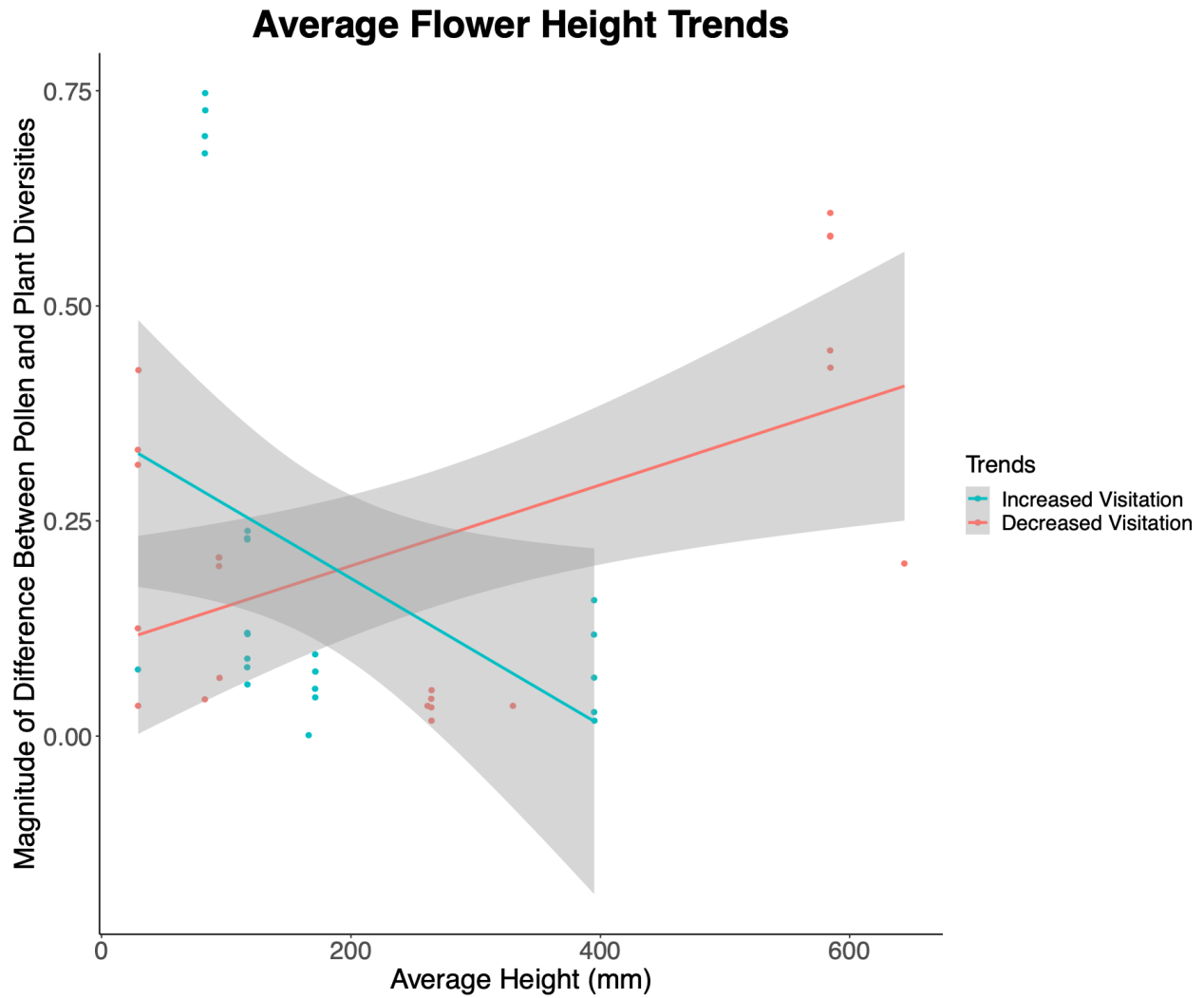


Figure 4. The blue trend line illustrates how average flower height has a large positive effect on the difference in pollen and plant diversities, while the red trend line illustrates how flower height has a sizable negative effect. The blue line indicates increased pollinator visitation frequency, and the red line indicates decreased pollinator visitation frequency.

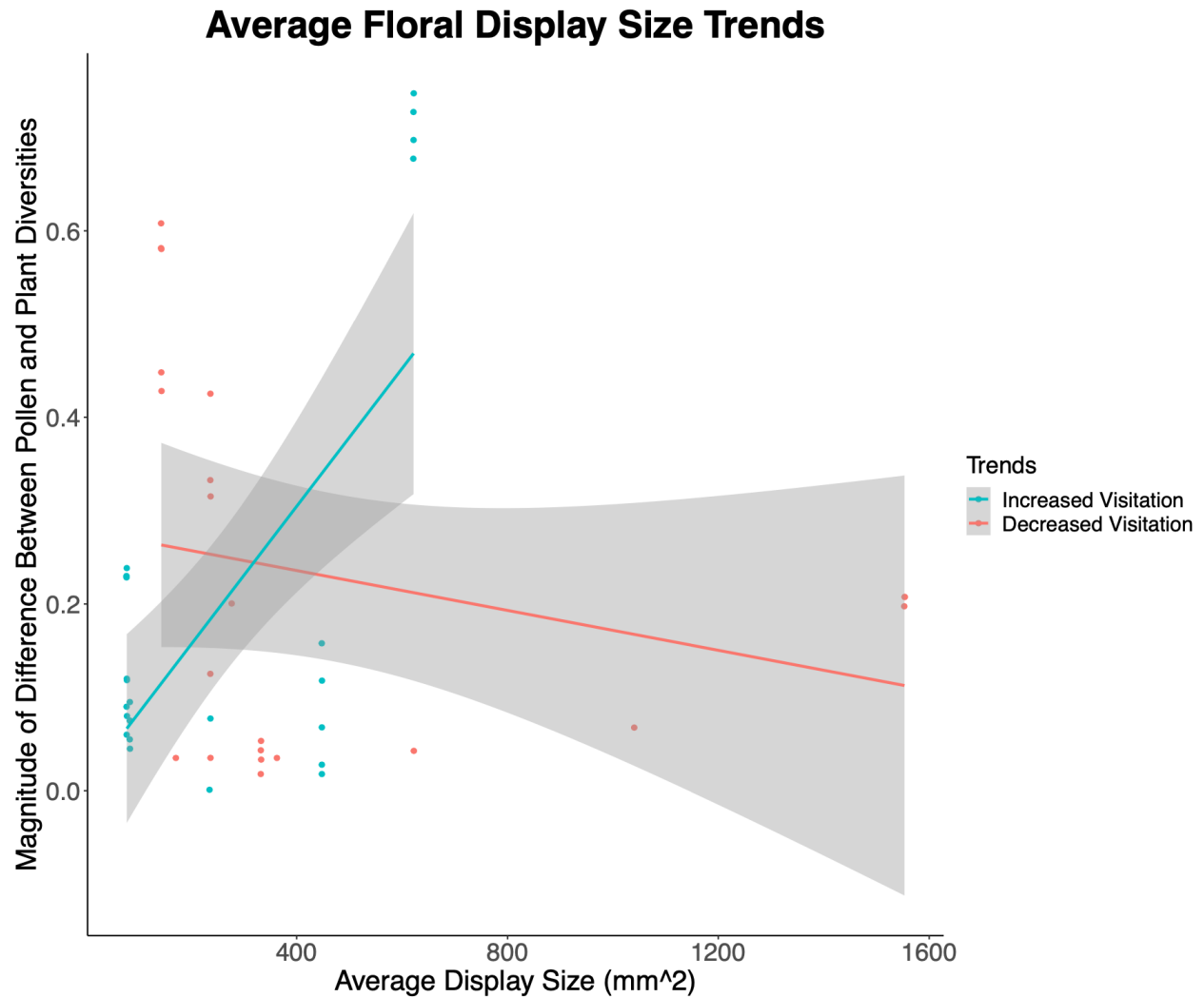


Figure 5. The blue trend line illustrates how average display size has a large positive effect on the difference in pollen and plant diversities, while the red trend line illustrates how display size has a fairly small negative effect. The blue line indicates increased pollinator visitation frequency, and the red line indicates decreased pollinator visitation frequency.

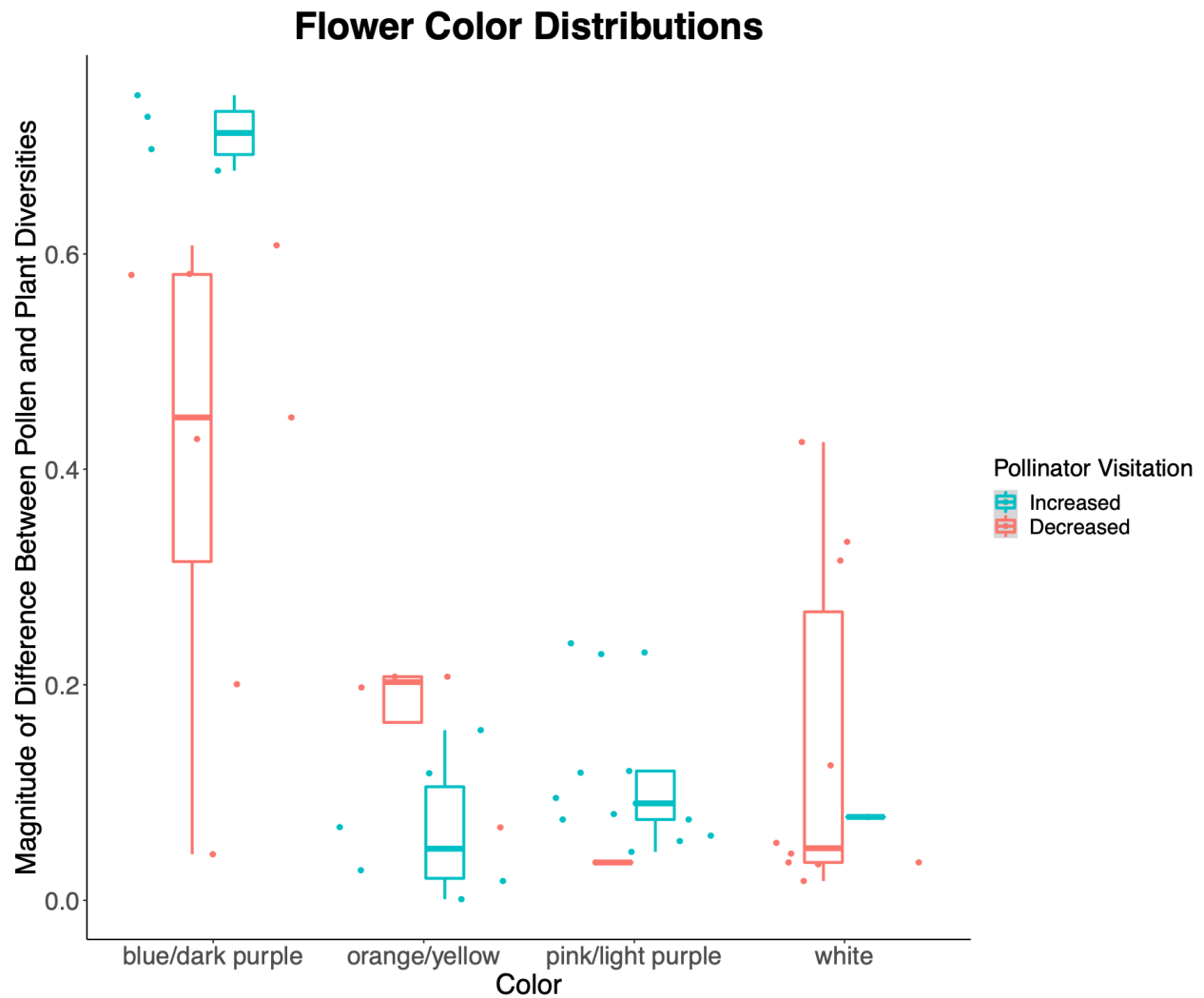


Figure 6. The blue box plots illustrate increased pollinator visitation frequency, while the red box plots illustrate decreased pollinator visitation frequency. All colors except pink/light purple have sizable decreased visitation distributions, and all colors except white have increased visitation distributions.