

The Effect of Dominant Floral Resource Removal on Plant-Pollinator Interactions

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Abstract

In order to understand the ecological and evolutionary significance of plant-pollinator mutualisms, it is critical to first comprehend the fluctuating and complex nature of plant-pollinator interactions. Specifically, it is important to realize how these interactions respond to changes in factors such as phenology, morphology, and abundance. To examine the effect of floral resource removal on plant-pollinator interactions, we removed a dominant floral resource, *Helianthella quinquenervis* (Asteraceae) from 10 plots. We paired each removal plot with a control plot and conducted paired plant-pollinator observations for 30 hours per week for 5 weeks. We then analyzed differences in pollinator visitation rates between control and removal plots using paired t-tests and linear mixed effects models. We found that overall pollinator visitation increases in response to resource availability. We also found that removal of *H. quinquenervis* facilitates the pollination of some plant species and competes for pollination with others.

Introduction

Nearly 90% of all flowering plant species rely on mutualistic animal pollinators for reproduction (Ollerton et al. 2011). Pollination mutualisms are highly dependent on factors of phenology, morphology and abundance in both plant and pollinator species (reviewed by Vázquez et al. 2009). Together these variables interact temporally and spatially to form complex communities. Interactions within communities are not static, but rather form and dissolve frequently and rapidly throughout a floral season (CaraDonna, et al 2017). It is essential to study the fluctuating and complex nature of plant-pollinator interactions in order to accurately learn the ecological and evolutionary significance of plant-pollinator mutualisms. Through observing plant-pollinator interactions within their community context, we can begin to understand the dynamic nature of ecological communities.

The presence or absence of floral resources can directly influence the pollination and reproductive success of co-flowering plant species that share pollinators within a community (e.g., Mitchell et al. 2009; Ogilvie and Thompson, 2016). We hypothesize that the removal of a dominant and abundant floral resource will result in an overall decrease in pollinator visitation rates relative to those present in natural floral communities. At the species level, if individual plants species are competing for pollinators with the removed resource, pollinator visitation will likely increase in removal plots in the absence of competition; subsequently, this would likely result in a decrease in reproductive success for these species. Alternatively, however, if the dominant floral resource draws in pollinators and these pollinators “spill over” to other plant species, visitation to co-flowering plant species may be greater in control plots relative to removal plots, which may increase species level reproductive success. Understanding how the removal of a major floral resource alters pollinator visitation rates and community composition is a critical first step in comprehending how plant-pollinator networks respond to change.

This study explored how plant-pollinator interactions respond to changes in the floral resource landscape. Specifically, we addressed this question through the removal of the dominant and abundant floral resource, *Helianthella quinquenervis* (Asteraceae) in a montane meadow ecosystem. We addressed two primary questions:

1) How do pollinator visitation rates vary between natural floral communities and communities where *H. quinquenervis* is removed? And 2) How does variation in visitation influence reproduction of different co-flowering plant species? Understanding how a drastic change in the floral landscape alters pollinator visitation rates and community composition is a critical first step to comprehending how plant-pollinator networks respond to various changes.

Methods

Study site & natural history

This experiment was conducted at The Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO, USA (38°57.5⁰ N, 106°59.3⁰ W, 2900 m a.s.l.). RMBL is surrounded by a diversity of ecosystems including dry and wet alpine meadows, coniferous forests, and aspen groves. Due to its high elevation, during most of the year the area is covered in snow and has a short summer growing period of roughly 3-5 months (CaraDonna, *et al.* 2014). Located about a mile south of the Gothic townsite is Maxfield Meadow, a dry montane alpine meadow with a total area of approximately 0.3 square kilometers. Maxfield Meadow contains a diversity of common perennial herbaceous wildflower species. The three most dominant co-flowering species for the duration of our study were *Helianthella quinquenervis* (Asteraceae), *Erigeron speciosus* (Asteraceae) and *Potentilla gracilis* (Rosaceae). *H. quinquenervis* is a self-incompatible Asteraceae with bright yellow composite flowers that are comprised of a central yellow disc that is 2-3 centimeters in diameter surrounded by ray flowers that make the total flower size up to 10 centimeters in diameter (Inouye, 1979). *E. speciosus* is another self-incompatible Asteraceae with 3-5 cm diameter composite flower heads made up of many lavender or pink rays surrounding a yellow disc (Allphin, *et al.* 2002). *P. gracilis* is a member of Rosaceae that is self-compatible, but benefits from pollination. The flowers are about 2-3 cm in diameter with 5 bright yellow petals and a whorl of approximately 20 stamens (Eriksen, 1996).

In this high altitude ecosystem, the phenology, or biological timing, of flowering events is very closely tied to the date of annual snowmelt (Inouye, 2008). Specifically, due to its high sensitivity to frost damage, the flowering success of *H. quinquenervis* is very tightly connected to the date of annual snowmelt. Lower snowpack levels result in accelerated melt off rates, which speed up the phenological timing of perennial wildflowers such as *H. quinquenervis*. This exposes such floral communities to the lower nighttime temperatures frequent in the earlier season, and subsequently increases their susceptibility to frosting events (Inouye, 2008). Phenological timing is one of the greatest bioindicators of the changing climate. As the impacts of climate change continue to worsen, it is critical to understand the cascading impacts that changes in resource availability may cause within dynamic ecological communities.

Experimental removal of Helianthella quinquenervis. My project utilized plots that were previously created by Dr. Amy Iler and Dr. Kailen Mooney. Plots were located in Maxfield Meadow, approximately one mile south of the Gothic townsite. We conducted our experiment in twenty paired control and removal plots spread out across the meadow (Fig 1& 2). In the removal plots, we removed all *H. quinquenervis* buds by clipping them off when they were approximately the size of a penny. We then

continued to remove new buds throughout the summer. Each circular macroplot measured 14 meters in diameter; within each macroplot there was a square 2x2 meter focal plot located in the center.

Plant-pollinator interaction observations. We conducted plant-pollinator observations in all plots for 5 weeks. We began observations approximately one week before the onset of *H. quinquenervis* and concluded observations approximately one week after its decline. Each week, we conducted 30 hours of plant-pollinator observations, which consisted of 15 hours of observations per treatment, and 1.5 hours per individual plot. Each plot received six 15-minute observation sessions per week.

The order of daily observations was randomly assigned. Each set of plant-pollinator interaction observations lasted 15 minutes and was always conducted by the same two researchers (R.G.D. and J.A.B) to prevent observation bias. All observations were paired so that each pair of control and removal plots were always sampled at the same time; researchers would switch between control and removal plots after each observation. During each observation session, we recorded all interactions that occurred between a pollinator and a plant species. Specifically, we recorded interactions where the pollinator came into contact with the reproductive structures of the plant.

Plant-pollinator observations occurred during peak pollinator activity, from approximately 0830–1700 during favorable weather conditions (*i.e.*, sunny, not raining and not too windy; *following* CaraDonna *et al.* 2017). To ensure adequate conditions, the following weather measurements were recorded before each observation period: minimum and maximum wind speed, temperature, relative humidity, and cloud cover.

Plants and pollinators were all identified following the same protocol as CaraDonna *et al.* (2017). Specifically, all flowering plants were identified to species, and all pollinators were identified to species or to the highest taxonomic classification possible. During field observations, pollinators were identified to either species or morphospecies. A reference specimen was collected for each morphospecies and later identified using the RMBL Entomology Reference Collection. Otherwise, pollinators were not collected during observations to avoid damage to natural populations levels (*following* CaraDonna *et al.* 2017).

Quantification of floral resources. To quantify differences in floral resource composition, we collected flowering phenology data every week for each 2x2 meter central focal plot. For all 22 flowering plant species present in our plots throughout the season, we counted either the number of flowers per stalk or the number of inflorescences (for species with many small flowers, *e.g.*, members of Asteraceae) (*following* CaraDonna *et al.* 2014). We also recorded the presence of plant species that were flowering outside of the 2x2 focal plot but still within the 14-meter diameter observation plot.

Quantification of plant reproduction for focal taxa. We collected fruits from two plant species dominant in control and removal plots: *P. gracilis* and *E. speciosus*. For

P. gracilis we collected 15 fruits per plant on 5 plants selected randomly from each plot. For *E. speciosus* we collected 15 capitula randomly selected from each plot. We used these collected fruits to determine an average seed set per plot for each plant species. For *P. gracilis* we counted the number of seeds on a subset of the total fruits collected from each plant and for *E. speciosus* we counted the number of seeds on a subset of the total capitula collected from each plot. All seeds from both plant species were dried and weighed.

Analyses. We examined differences in response variables (pollinator visitation rates, fruit set, seed set, pollinator community composition) between control and removal treatments using linear mixed effects models (using the package lme4 in R statistical framework). Our analyses are analogous to a t-test, but account for the repeated sampling of plant-pollinator interactions at each plot during each week. We ran separate analyses for each of the five weeks of plant-pollinator interaction observations. First, we ran analyses for raw visitation rates per minute for control versus removal plots for each week. Then, to account for floral resource abundance we ran analyses on visitation rates per minute per flower for each week. To further examine visitation to co-flowering plant species, we excluded *H. quinquenervis* visitation data and ran the same analyses (raw visitation per minute as well as visitation per minute per flower); we excluded week 1 because no *H. quinquenervis* was in bloom during that time. We then isolated the visitation data from our most abundant and dominant focal co-flowering plant species, *E. speciosus* and *P. gracilis*. We analyzed differences in visitation between control and removal plots for each species independently for all weeks that the respective flower was in bloom (weeks 2-5 for *P. gracilis* and weeks 3-5 for *E. speciosus*).

Results

To initially compare overall pollinator visitation rates between control and removal treatments, we analyzed the raw visitation rate data, which is simply pollinator visitation per minute per plot. As expected, visitation rates were not significantly different in week 1, when there was no *H. quinquenervis* yet in bloom (Table 1). Similarly, visitation rates were not significantly different in weeks 4 or 5, when *H. quinquenervis* floral abundance was in significant decline (Table 1). As expected, visitation rates during peak flowering (weeks 2 and 3) were significantly higher in the *H. quinquenervis* control plots (week 2: *control* = 1.28, *removal* = 0.697, $t = 4.61$, $p < 0.001$; week 3: *control* = 2.19, *removal* = 1.37, $t = 3.69$, $p < 0.001$; Table 1; Fig. 3).

After finding this initial difference in raw visitation rates, we examined whether we could attribute this pattern to resource availability: were control plots receiving higher visitation rates during peak flowering simply because they had more flowers present at any given time than removal plots? To address this question we scaled pollinator visits per minute to the number of flowers blooming per plot through incorporating our weekly flowering phenology data (i.e., visits per minute per flower per plot). After accounting for floral abundance, the difference in raw visitation rates per plot diminished (visits per minute per flower: week 2, *control* = 0.0295, *removal* = 0.0303, $t = 0.164$, $p = 0.8701$; week 3, *control* = 0.0373, *removal* = 0.0314, $t = 1.09$, $p = 0.280$; Table 1, Fig. 4). These analyses suggest that pollinator visitation rates increased at least partly

in response to the increase in resource availability (i.e., more *H. quinquenervis* flowers) in the control plots.

Next, we examined further the differences in pollinator visitation rates between different co-flowering plant species in control and removal plots. In order to do so, we had to first understand visitation rates in the floral communities in the absence of *H. quinquenervis*; in other words, how do pollinator visitation rates compare between treatments when all visits to *H. quinquenervis* are removed? Without *H. quinquenervis*, we found that removal plots received significantly higher visitation rates during the first week of peak flowering. However, visitation rates during the second week of peak flowering were not significantly different (week 2: *control* = 0.0162, *removal* = 0.0308, $t = -3.04$, $p = 3.166 \times 10^{-3}$; week 3: *control* = 0.0272, *removal* = 0.0325, $t = -0.856$, $p = 0.3940$; Table 1, Fig. 5)

To examine where this significant difference was coming from, we peeled back yet another layer of data and isolated and analyzed visitation data from the two most dominant co-flowering plant species in the meadow, *P. gracilis* and *E. speciosus*. *P. gracilis* began flowering at the start of the experiment, while *E. speciosus* did not begin flowering until week 3. Overall, we found that *P. gracilis* received significantly higher visitation rates in the removal plots during both weeks of peak flowering (week 2: *control* = 0.0238, *removal* = 0.0449, $t = -2.3095$, $p = 0.0236$; week 3: *control* = 0.0292, *removal* = 0.0652, $t = -2.21$, $p = 0.03056$; Table 1, Fig. 6). No significant differences were present in visitation rates to *P. gracilis* in control versus removal plots during weeks 4 and 5 (the decline of *H. quinquenervis*).

Conversely, we found that *E. speciosus* received higher visitation rates in the control plots during the second week of peak flowering (week 3: *control* = 0.107, *removal* = 0.0371, $t = 2.15$, $p = 0.03813$; Table 1, Fig. 7). Similar to *P. gracilis*, during weeks 4 and 5 (the decline of *H. quinquenervis*), there were no significant differences in visitation rates to *E. speciosus* between control and removal plots.

Discussion

We examined how the removal of a dominant and abundant floral resource affected plant-pollinator interactions in a montane meadow in the Colorado Rocky Mountains, USA. Specifically, we explored two main questions: i) How do pollinator visitation rates vary between natural, intact floral communities and communities where *Helianthella quinquenervis* is removed? And ii) How does variation in visitation influence reproduction of different co-flowering plant species? We hypothesized that the removal of a dominant and abundant floral resource would result in an overall decrease in pollinator visitation rates relative to those present in natural floral communities (Mitchell *et al.* 2009). At the community level, we found evidence consistent with this hypothesis, that overall visitation rates were indeed greater in the presence of a dominant and abundant floral resource. However, this pattern appears to be at least partly driven by differences in floral abundance. At the individual species level, and consistent with our species-specific hypothesis, we found contrasting patterns between the two other dominant co-flowering plants in this community. *Potentilla gracilis* experienced decreases in pollinator visitation in the presence of *H. quinquenervis* (control plots), whereas *Erigeron speciosus* experienced increases. Therefore, our experiment suggests that *H. quinquenervis* has a competitive

effect on pollinator visitation of *P. gracilis*, whereas it has a facilitative effect on the pollinator visitation to *E. speciosus*.

As expected, we saw no difference between the visitation of co-flowering plant species in control versus removal plots when *H. quinquenervis* was not flowering or was in low abundance. The only significant visitation differences to co-flowering plant species occurred during peak flowering of *H. quinquenervis* (weeks 2 and 3). After removing all *H. quinquenervis* interactions from the data during peak flowering, we see that there was a significant difference in visitation to control and removal plots only during week two. This difference disappears in week three, likely because that is the week that the new resource *E. speciosus* became abundant and dominant. This new species likely “evens out” overall visitation to control and removal plots across the landscape.

The removal of *H. quinquenervis* during peak flowering facilitates the pollinator visitation of *E. speciosus* and competes for pollinator visitation with *P. gracilis* (Table 1, Fig 6&7). This finding shows that the presence or absence of a dominant floral resource can strongly influence the pollination and reproductive success of co-flowering plant species that share pollinators within a floral community. There are several explanations for this result: i) pollinators exercise site-fidelity, so removal of *H. quinquenervis* increases pollinator visitation to plant species within removal plots, ii) abandonment behavior of pollinators decreases overall visitation within *H. quinquenervis* removal plots, iii) *H. quinquenervis* acts as a “magnet plant” and its pollinators spill over to increase the pollination rates of co-flowering plant species, and iv) similarities in floral morphologies attract similar pollinator communities and thus increase pollination to co-flowering plant species.

The removal or decline of a pollinator-dependent floral resource such as *H. quinquenervis* may result in site-fidelity of individual pollinators, and a subsequent predicted increase in co-flowering plants’ reproductive successes (Ogilvie and Thompson, 2016; Brosi and Briggs, 2013). For instance, if pollinator communities were similar between *H. quinquenervis* and *P. gracilis*, and pollinators exercised site-fidelity within removal plots, we would expect an increase in visitation to *P. gracilis* in the absence of *H. quinquenervis*. The removal of *H. quinquenervis* also has the potential to cause pollinators to abandon removal plots and search for the floral resource elsewhere (Ogilvie and Thompson, 2016; Brosi and Briggs, 2013). If pollinators are foraging for *H. quinquenervis* and *E. speciosus* during the same foraging bouts, abandonment of removal plots due to the lack of *H. quinquenervis* could explain why *E. speciosus* receives lower visitation rates in removal plots.

H. quinquenervis may act as a magnet plant within the floral community; when pollinators begin a foraging bout on *H. quinquenervis* they may end up “spilling over” to the other co-flowering species close by. This spill-over effect may be tightly linked to floral morphology. *H. quinquenervis* and *E. speciosus* are both in the family Asteraceae, and have similar yellow display centers formed from many disc flowers. This shared visual cue might serve as an explanation for why pollinators tend to visit more *E. speciosus* in control plots than removal plots. Pollinators may begin a foraging bout on either *H. quinquenervis* or *E. speciosus* and end up “spilling over” to the other dominant Asteraceae that is nearby and available for pollination.

Conversely to *E. speciosus*, *P. gracilis* receives significantly lower visitation in control plots than removal plots during peak flowering of *H. quinquenervis*. *P. gracilis* is a member of the Rosaceae family and has a significantly different floral morphology than that of both *H. quinquenervis* and *E. speciosus*. Although *P. gracilis* is also yellow, it is not a composite, and thus does not have a large center made up of disc flowers. Pollinators are attracted to the center of flowers, where the floral rewards of nectar and or pollen are contained. This clear visual and morphological difference between the reward centers of *P. gracilis* and the two members of the Asteraceae family may be an important reason for why there is not a “spillover” effect present between *H. quinquenervis* and *P. gracilis*. If pollinators are effective in foraging on an Asteraceae plant, it makes energetic sense for them to visit multiple plant species with similar morphology in a foraging bout. Pollinators have to forage for nectar and pollen very differently on *P. gracilis*, so it may not make sense for them to visit it on the same foraging bout they are making to members of the Asteraceae family. Therefore, in the absence of *H. quinquenervis*, pollinators might focus more specifically on the pollination of *P. gracilis*, and thus increase its visitation rates in removal plots relative to control plots. Future analyses of pollinator community abundance, diversity and turnover will help us to realize whether pollinator fidelity and spillover are indeed driving these differences in visitation between co-flowering plant species.

Understanding how the removal of a dominant floral resource alters pollinator visitation rates and community composition is a critical first step to comprehending how plant-pollinator networks respond to various changes (Brosi, et al 2017). Although we cannot use this study to directly predict what will happen during a year when *H. quinquenervis* is more susceptible to early season frosting events (Inouye 2008), we can use these data to understand the cascading effects that resource removal may have on interactions between co-flowering plant species and their pollinators (Mitchell *et al* 2009). It is clear that the removal of a single, but dominant floral resource does indeed influence patterns of plant-pollinator interactions in various ways, resulting in what appears to be both competitive and facilitative effects. As the effects of climate change continue to worsen, it is critical that we gain a basic understanding of how changes in phenology and abundance may drive the dynamics of plant-pollinator interactions (CaraDonna *et al* 2014).

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Tables and Figures

Table 1 Mean visitation in control and removal plots and t-values and p-values for different subsets of data scaled to visits per minute or visits per flower per minute. All values were computed using a Welch Two Sample T-test (R statistical software). Analyses with significant p-values ($p < 0.05$) are displayed in bolded font. All data (weeks 1-5) were subset (All, No HQ, *P. gracilis*, and *E. speciosus*) and analyzed accordingly when possible. Dashes indicate weeks where analyses was not appropriate (e.g., *E. speciosus* was not flowering in weeks 1 and 2).

Scale of pollinator visitation	Data included in analysis	Week #	Mean visitation control	Mean visitation removal	t-value	p-value
Visits/min	All	1	0.584	0.705	-0.767	0.4457
Visits/min	All	2	1.28	0.697	4.61	<0.0001
Visits/min	All	3	2.19	1.37	3.69	<0.0001
Visits/min	All	4	0.584	0.704	-0.767	0.4457
Visits/min	All	5	0.618	0.705	-0.529	0.5983
Visits/flower/min	All	1	0.009880	0.01647	-1.91	0.06008
Visits/flower/min	All	2	0.0295	0.0303	0.164	0.8701
Visits/flower/min	All	3	0.0373	0.0314	1.09	0.2800
Visits/flower/min	All	4	0.00464	0.00558	-0.813	0.419
Visits/flower/min	All	5	0.0105	0.0156	-1.41	0.164
Visits/flower/min	No HQ	1	-	-	-	-
Visits/flower/min	No HQ	2	0.0162,	0.0308	-3.04	3.166×10^{-3}
Visits/flower/min	No HQ	3	0.0272	0.0325	-0.856	0.3940
Visits/flower/min	No HQ	4	0.00519	0.00559	-0.330	0.7426
Visits/flower/min	No HQ	5	0.0108	0.0156	-1.31	0.195
Visits/flower/min	<i>P. gracilis</i>	1	-	-	-	-
Visits/flower/min	<i>P. gracilis</i>	2	0.0238	0.0449	-2.31	0.02360
Visits/flower/min	<i>P. gracilis</i>	3	0.0292	0.0652	-2.21	0.03056
Visits/flower/min	<i>P. gracilis</i>	4	0.0132	0.0214	-1.7564	0.08454
Visits/flower/min	<i>P. gracilis</i>	5	0.113	0.168	-0.91928	0.3622
Visits/flower/min	<i>E. speciosus</i>	1	-	-	-	-
Visits/flower/min	<i>E. speciosus</i>	2	-	-	-	-
Visits/flower/min	<i>E. speciosus</i>	3	0.107	0.0371	2.15	0.03813
Visits/flower/min	<i>E. speciosus</i>	4	0.0108	0.00832	1.1432	0.2571
Visits/flower/min	<i>E. speciosus</i>	5	0.0180	0.0215	-0.641	0.524

Maxfield Meadow Plot Map

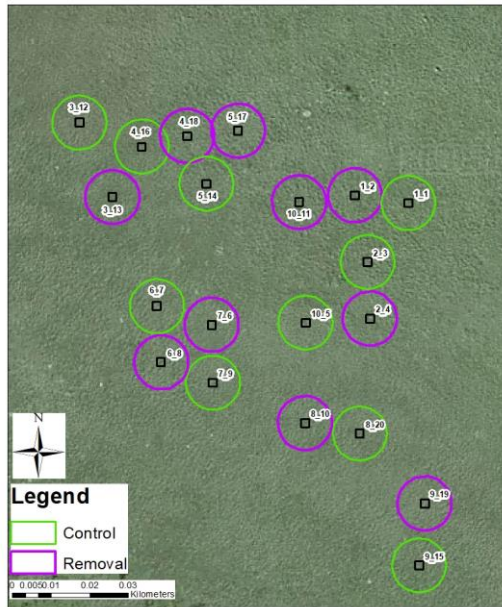


Figure 1 Plot map of Maxfield Meadow. Green circles indicate control plots, and purple indicate removal plots. The first number in the label represents the plot pair number (all removal and control plots are paired) and the second is the individual plot identification number.

Maxfield Meadow

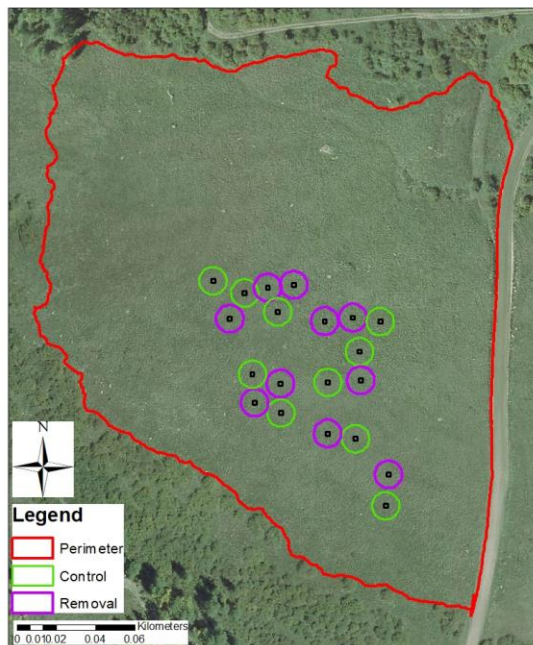


Figure 2 Vicinity map of Maxfield Meadow. All green circles are control plots and purple are removal plots. The red line represents the perimeter of Maxfield Meadow.

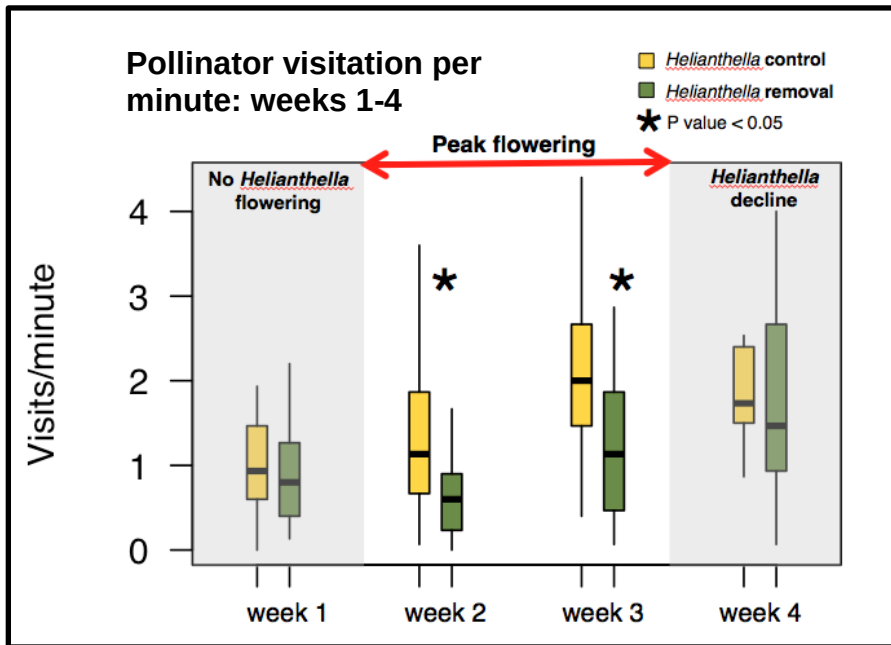


Figure 3 Pollinator visits per minute on all flowers during weeks 1-4. Yellow bars represent control plots and green bars represent removal plots. Asterisks indicate significant differences in visitation rates during week 2 and 3 (peak flowering) between control and removal plots ($p < 0.05$, see Table 1 for specific values).

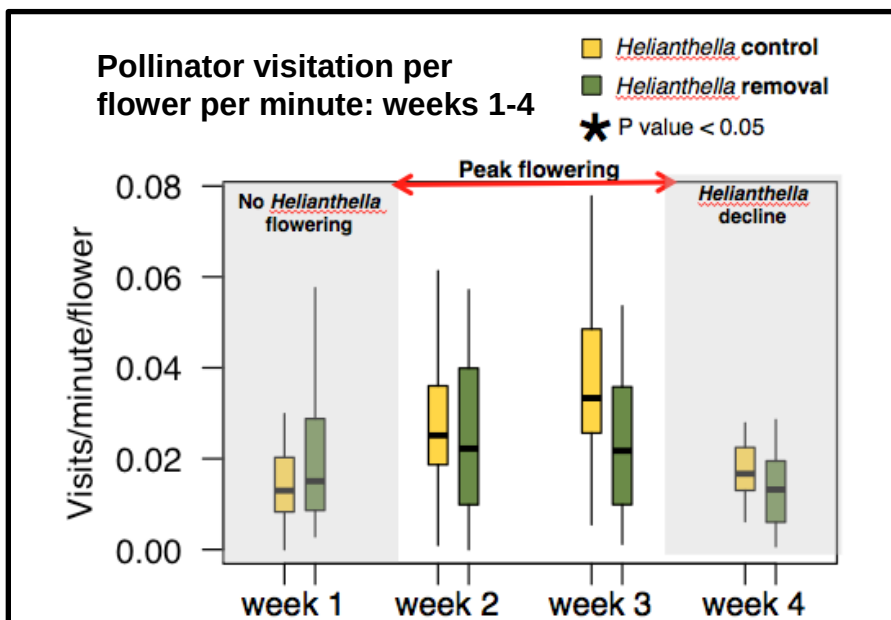


Figure 4 Pollinator visits per flower per minute on all flowers during weeks 1-4. Yellow bars represent control plots and green bars represent removal plots. No asterisks are present, indicating that there no significant differences exist between control and removal plots in visitation per minute per flower ($p < 0.05$, see Table 1 for specific values).

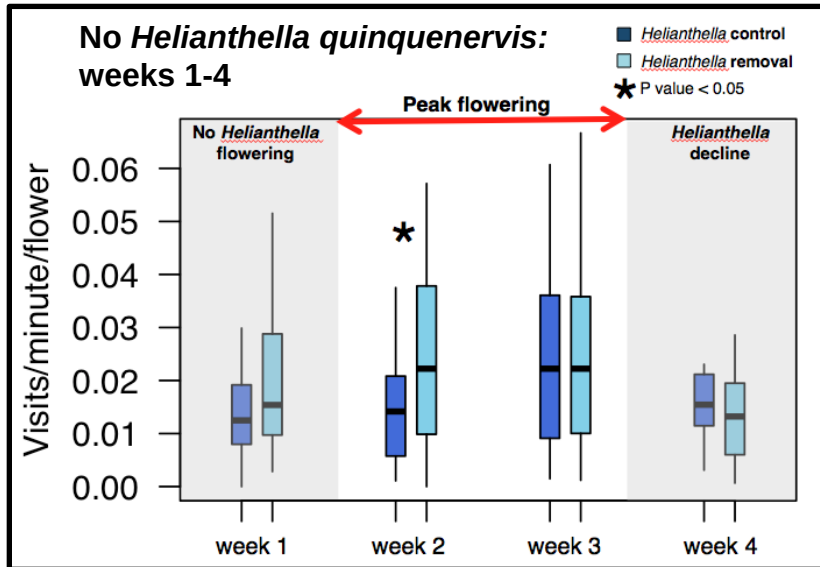


Figure 5 Pollinator visits per minute per flower with no *Helianthella quinquenervis* data during weeks 1-4. Dark blue bars represent control plots and light blue bars represent removal plots. Asterisk indicates a significant difference in visitation rates during week 2 (peak flowering) between control and removal plots ($p < 0.05$, see Table 1 for specific values).

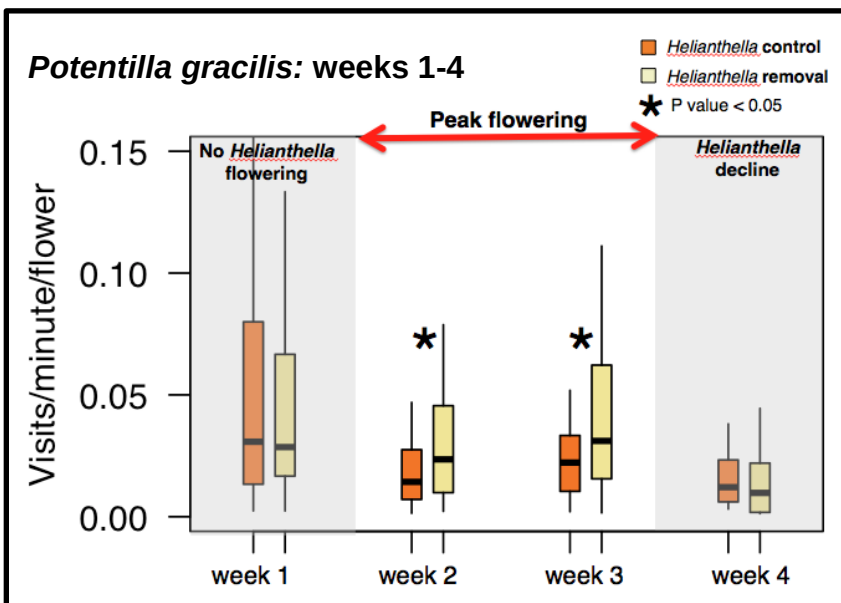


Figure 6 Pollinator visits per minute per flower for *Potentilla gracilis* only during weeks 1-4. Orange bars represent control plots and yellow bars represent removal plots. Asterisks indicate significant differences in visitation rates during week 2 and 3 (peak flowering) between control and removal plots ($p < 0.05$, see Table 1 for specific values).

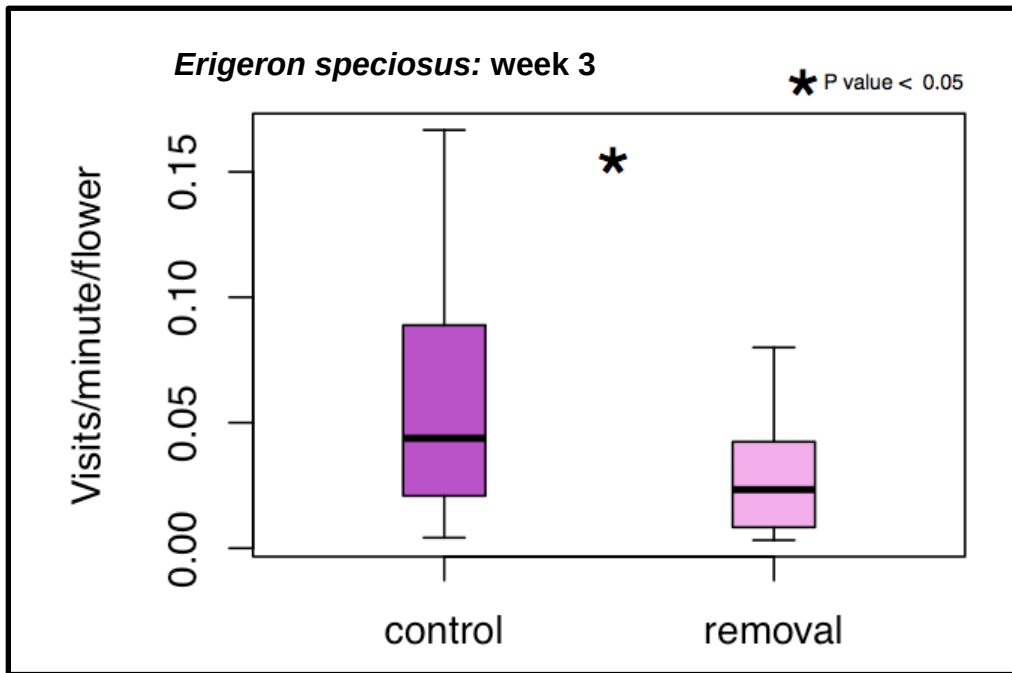


Figure 7 Pollinator visits per minute per flower for *Erigeron speciosus* only during week 3. Dark purple represents the control plot, while light purple represents the removal plot. The asterisk indicates a significant difference in visitation between the control and removal plot ($p < 0.05$, see Table 1 for specific values).