ABSTRACT

THE EFFECTS OF FLOWER PATCH DENSITY ON POLLINATOR VISITATION

by Tristan Alexander Barley

There is conflicting research regarding how conspecific density can affect pollinator visitation, with some studies indicating dense flower patches will receive more visitors and other studies demonstrating the opposite. This study investigated the effects of conspecific density on pollinator visitation in a restored prairie. Three plant species, *Penstemon digitalis*, *Monarda fistulosa*, and *Eryngium yuccifolium*, were used, with visiting pollinators and their behaviors recorded. Conspecific density did not have an effect on visitation rates for *P. digitalis* ($p = 0.07$), *M. fistulosa* ($p = 0.67$), or *E. yuccifolium* ($p = 0.07$). These results suggest that conspecific density may only be relevant to visitation rates in certain plant species. However, different genera of pollinators did show varying responses to flower density. This suggests that pollinators are not monolithic and that isolation may impact certain pollinators differently than others. Furthermore, a comparison of seed weight demonstrated that *E. yuccifolium* plants tended to have larger seed sets in isolated individuals ($p = 0.0003$), indicating that flowers in large patches may be pollinated less effectively and are competing for, rather than facilitating, pollinator visits.

THE EFFECTS OF FLOWER PATCH DENSITY ON POLLINATOR VISITATION

Thesis

Submitted to the
Faculty of Miami University
in partial fulfillment of
the requirements for the degree of
Master of Environmental Science

by

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Miami University
Oxford, Ohio
2020

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This Thesis titled

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has been approved for publication by

The College of Arts and Sciences

and

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Acknowledgements

The authors would like to thank Drs. Donna McCollum and R. Hays Cummins for the use of their property as well as their advice, Dr. Ann Rypstra for her feedback on this research, Mike Minnick for his aid in identifying bees, and Alex Bowers and Sarah Jaramillo for their help in data collection.

Introduction

Pollinator visitation is density dependent in some instances, with pollinator choices determined by the density of flowering plants (Silander, 1978; Sih and Baltus, 1987; Kunin, 1993; Kunin, 1997; Ison and Wagenius, 2014). Large patches of flowers may be preferable to pollinators because dense patches of flowering plants will reduce flight times between flowers and, therefore, pollinators will use less energy while foraging. However, some research has shown that pollinator visitation does not disproportionately increase with isolation (Feldman, 2006; Steven *et al*., 2003; Johnson, Hollen, and Kuhlmann, 2012), or in some cases it actually increases (Wagenius and Lyon, 2010). This suggests that flowers compete for pollinators when plants are at high densities (Steven *et al*., 2003; Feldman, 2006; Johnson, Hollen, and Kuhlmann, 2012). While larger patches can attract more pollinators overall, smaller patches have less competition, resulting in more pollinator visits per plant (Steven *et al*., 2003; Feldman, 2006; Johnson, Hollen, and Kuhlmann, 2012). This conflicting research suggests that pollinator choices are more complex than simply selecting the largest flowering patches, with other variables possibly driving these interactions with plant communities.

One explanation for the conflicting research regarding how isolation can affect pollinator visitation lies in behavioral differences between pollinator groups. The identity of the pollinator can be relevant to how isolation will affect visitation rates, with studies showing that *Bombus* spp. tend to have higher visitation rates in denser patches, while other groups have lower visitation in those same patches (Sih and Baltus, 1987; Grindeland, Sletvold, and Ims, 2005). Notably, solitary bees (Halictidae) have been shown to visit larger patches less often in comparison (Sih and Baltus, 1987). These trends do not apply solely to bee species, with other pollinator groups, such as flies, being found to also exhibit similar patch preferences (Johnson, Hollen, and Kuhlmann, 2012). However, there are few studies explicitly investigating these behavioral patterns, with most studies simply investigating one pollinator group visiting one particular plant species rather than accounting for the whole of the pollinator and plant community. Given the current extent of studies on pollinator behavior and the effects of patch density, more research is needed to determine if these different visitation patterns are consistent across pollinator species and whether they are further driven by the identity of the plant being visited.

This study investigated pollinator visitation in a restored tallgrass prairie. Prairies are diverse ecosystems that have suffered from extensive human alteration, and as a result of this destruction, the U.S. is experiencing the loss and endangerment of many prairie plant and animal species (Samson and Knopf, 1994). With vast stretches of these rare systems being impacted by human development and agriculture, it is vitally important to maintain the diversity of remaining prairies and ones that have been restored. This can be especially problematic in restored prairie systems since some plant species can have small, fragmented communities (Maina and Howe, 2000). These isolated plants or patches of plants may suffer from a reduced seed set as a result of lack of pollen transfer from pollinator visitation (Argen, 1996; Jennersten, 1988; Fischer and Matthies, 1998). This can cause an Allee effect, resulting in a decline in per capita growth rate of the population, further reducing the fitness of these individuals (Allee *et al*., 1949; Menges, 1991; Ouborg and Van Treuren, 1994; Groom, 1998; Wagenius, 2006). The fitness of these small plant populations may be limited by the availability of pollen from nearby conspecifics and the visitation rates by pollinating insects. While pollen limitation and the density dependence of pollination rates has been highlighted in previous studies, there is a lack of research regarding how these can affect populations in restored prairies. With the tendency for these habitats to form isolated flowering communities, and the importance of conserving them, research on pollinator behavior in this setting can provide a natural means of investigating visitation in isolated patches with practical conservation implications, such as selectively planting forbs closer or farther apart to support outcrossing.

We investigated how isolation of plants from conspecifics could affect pollinator visitation in a restored tallgrass prairie. We predicted that isolation would result in a reduction in pollinator visitation, as larger patches should provide a more efficient means of foraging for pollinators, reducing their overall travel since they can remain in a larger patch longer than they would in a smaller one. However, density was predicted to affect pollinators differently based on the identity of the pollinator. Given that *Bombus* spp. have been shown to visit larger patches more frequently (Sih and Baltus, 1987; Grindeland, Sletvold, and Ims, 2005), this pattern was expected to continue, with solitary bees having decreased visitation to these patches (Sih and

Baltus, 1987). The effects on plant fitness followed these field observations. Seed production in one of the investigated flowering prairie species was examined to ascertain whether or not these plants were pollen limited; if increasing isolation results in a decrease in visitation, isolated plants should have a reduced seed set as a result. Given the lack of clarity on whether isolation increases pollinator visitation (Silander, 1978; Sih and Baltus, 1987; Kunin, 1997; Ison and Wagenius, 2014) or decreases it (Wagenius and Lyon, 2010), and whether these differences could stem from pollinator species, this study will help to illuminate the effects of isolation in a restored prairie system, better informing how flowering communities are planted in prairie restorations and managed in the future.

Methods

Study Site and Plant Species

This study was conducted at the Edge of the Farm Conservation Area, located near Oxford, Ohio (Coordinates: 39.452843, -84.734984). The property contains 32 acres of conserved land, consisting of forests, wetlands, and 11 acres of restored prairie. The site was historically farmland, but restoration began 10 years before our study. The prairie site consisted of former agricultural fields sown with 10 grass species and 21 different forb species, including the plants used in our study. Since the initiation of restoration, the site has been maintained through selective bush hogging and invasive species spraying. Data collection was undertaken from May to August of 2019. Three plant species were observed during this study: *Penstemon digitalis* (beardtongue), *Monarda fistulosa* (bee balm), and *Eryngium yuccifolium* (rattlesnake master). Both *M. fistulosa* and *E. yuccifolium* were selected due to reproducing primarily through obligate outcrossing, though *E. yuccifolium* does have a small degree of self-compatibility (Cruden, Hermanutz, and Shuttleworth, 1984; Molano-Flores, 2001). The final species, *P. digitalis*, while capable of self-pollination, generates greater seed sets when pollinated by insect pollinators (Clinebell II and Bernhardt, 1998; Zorn-Arnold and Howe, 2007). Furthermore, the starting bloom times of these species do not overlap, with *P. digitalis* blooming in the late spring, *M. fistulosa* blooming in early-mid summer, and *E. yuccifolium* blooming in late summer. This allowed data to be collected from each while the others had not yet begun to bloom or had ceased to attract pollinators.

Pollinator Observations and Seed Collections

Observational sampling efforts were undertaken with individual plants. Each individual was marked with an inconspicuous, clear tag; flowers (*P. digitalis*) or inflorescences (*M. fistulosa, E. yuccifolium*) on each plant were counted and height (cm) was recorded. Observational efforts consisted of watching each plant individually for a five-minute period, recording all pollinator visitors and their behaviors. Pollinators were noted when they landed on a(n) flower/inflorescence, interacted with the flower/inflorescence by foraging for nectar, and when they visited multiple flowers/inflorescences on the same plant. For *P. digitalis* and *M. fistulosa*, two sampling efforts were completed for each individual plant, for a total of 10 minutes of observation. Due to the high prevalence of zero visits from these data sets, *E. yuccifolium* was observed three times, for 15 minutes of observation total, to produce a more representative sample. Plants that were damaged or did not undergo the full observational sampling effort were not used in the dataset. All data collection took place between 10am and 4pm and was conducted from June 7-12 for *P. digitalis*, July 3 for *M. fistulosa*, and July 24-26 for *E. yuccifolium*.

After completion of observational efforts, so as not to interfere with pollinator visits, a two-hour sampling effort was conducted for each plant species to collect visiting pollinators. Any insects that visited our focal plant species were collected. This was done to collect as many pollinator species visiting the target plants as possible to fully characterize the community. Larger pollinators were captured utilizing an insect net, and an aspirator was used to capture smaller individuals. Pollinators collected consisted of any insects that were observed to visit the study plant species, and included bees, beetles, and wasp species. All bees collected were identified down to the species level, while other pollinators were identified to the family or genus level.

Seed sets from *E. yuccifolium* were collected after pollinator observation and collection efforts were completed. Seeds were determined to be mature in November of 2019 and were collected during that time; plants that had clearly been damaged or had lost seeds due to herbivory were not used in data analysis. Twenty plants were randomly selected to be covered with mesh pollinator exclusion bags to test if visits from pollinators were required for reproduction. These bags were placed to cover all inflorescences in July of 2019, prior to individual flowers reaching reproductive maturity. Seeds were weighed in grams and divided by the total number of inflorescences.

Spatial and Data Analysis

The GPS coordinates for individual plants were collected for use in ArcMap using the ArcGIS Collector app. GPS coordinates for all individuals within 50 meters of the selected plants for sampling were collected for density analysis. Maps were generated to determine conspecific density and distance to forest edge (Fig. 1). Density, or patch size, was described as the number of conspecifics within 5 meters of each individual, a metric used in previous studies investigating flowering plant isolation and density which demonstrated that local abundance of flowers, rather than total population, was more important to reproduction (Sih and Baltus, 1987; Wagenius, 2006). Given the size of the prairie, as well as the GPS sensitivity used to record plant locations being ~6 feet, larger buffer zones to determine density would likely increase the patch size to make all patches indiscernible from one another, while smaller would likely be too fine for the GPS sensitivity to pick up. Distance to forest edge for each individual was also measured for analysis. Linear models were created in RStudio predicting pollinator visitation from distance to forest edge, conspecific density, flower/inflorescence counts, and plant height to determine if there was a relationship between these factors and pollinator visits. Generalized linear models with Poisson distributions were created for datasets that required it due to a left skew. To account for the fact that larger plants with more flowers may receive more visitors simply through having more flowers, a ratio of pollinator visits ÷ flower/inflorescence count, or visits per flower, was also used as a response variable, with conspecific density, plant height, and distance to forest edge used as predictor variables.

Visitation results were further investigated through breaking down how conspecific density affected different pollinator species. For each plant species, pollinators were broken down by genus, family, or designated as “other” if they represented a genus or family group that had few visitors. The visitation rates of these pollinator groups, which comprised the most abundant pollinators and those designated as “other”, were then compared to conspecific density. MANOVA tests were run on all pollinator groups for each plant species, with the models predicting visitation for each group from conspecific density, flower/inflorescence count, and plant height, with follow up linear models conducted to confirm significant MANOVA results. A linear model was also created using *E. yuccifolium* seed weight per inflorescence (total seed weight for each plant ÷ total inflorescence count) with predictor variables of conspecific density, pollinator visitation, and plant height to determine if these variables influenced seed set weight.

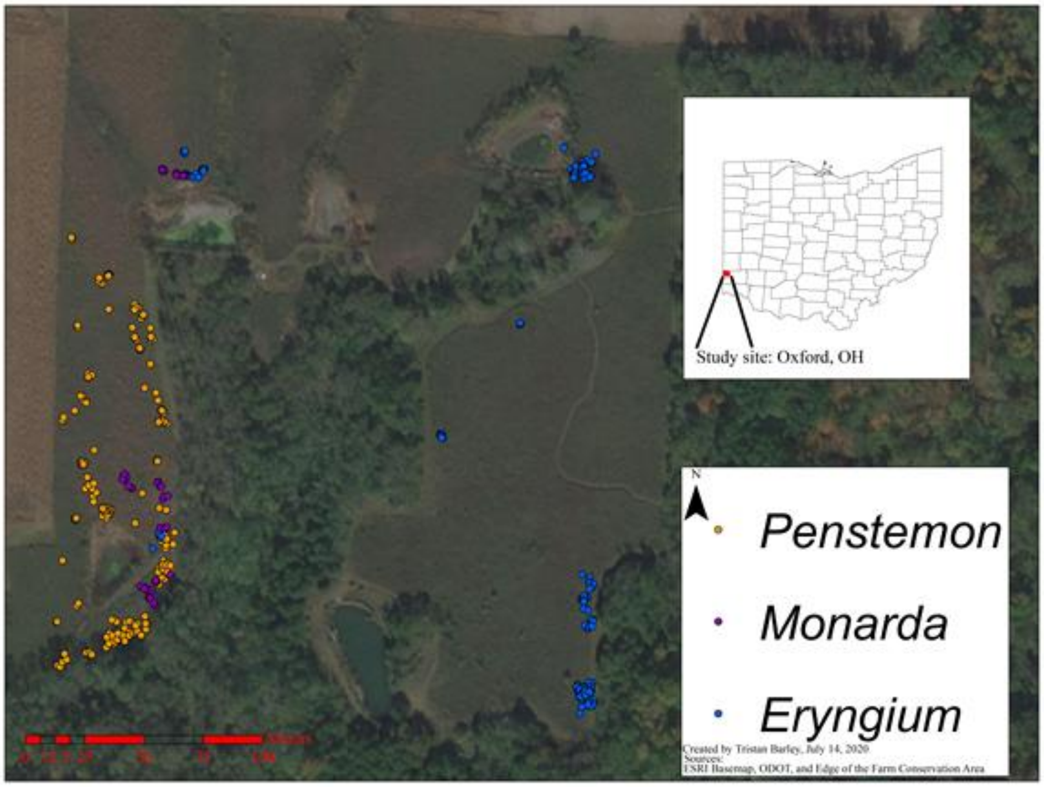

Fig. 1.—Location of individual *P. digitalis* (n = 268), *M. fistulosa* (n = 51), and *E. yuccifolium* (n = 182) within the tallgrass prairie at the Edge of the Farm Conservation Area used for pollinator observations. GPS points of individuals that were in the prairies, but not used for data collection, were also collected for density analyses and are not represented in this figure.

Results

Pollinator Visitation

The effect of conspecific density on pollinator visitation varied among the study species. Both *P. digitalis* and *E. yuccifolium* had weak positive relationships between conspecific density and pollinator visitation ($p = 0.071$ and 0.066, Table 1). For *M. fistulosa,* there was no relationship between conspecific density and pollinator visitation ($p = 0.672$, Table 1). Furthermore, linear models utilizing the visits per flower as predictors of pollinator visitation were insignificant for all plants ($p > 0.05$).

The full models investigating the effects of flower/inflorescence count, plant height, distance to forest edge, and conspecific density were all significant ($p < 0.001$, Table 1). However, that was largely driven by flower/inflorescence count, as pollinator visitation increased with the flower/inflorescence counts ($p < 0.05$, Table 1). Visitation tended to increase with height for both *P. digitalis* and *E. yuccifolium* ($p = 0.006$ and 0.028, Table 1), but decreased in *M. fistulosa* ($p = 0.222$, Table 1). Distance to the edge of the nearby forest had no effect on pollinator visitation for all plants, despite the majority of the pollinators collected during sampling being forest nesting species (Table 4). The greatest disparity between the models was present in the R-squared values, with the *E. yuccifolium* model explaining the least variation in the dataset ($r^2 = 0.251$, Table 1) while the *M. fistulosa* model explained almost all of the variation present in the dataset ($r^2 = 0.918$, Table 1).

Conspecific density, however, increased or decreased visitation based on the identity of the visiting pollinator. MANOVA tests showed that pollinator visitation varied with conspecific density, flower/inflorescence count, and plant height (Table 2). Follow-up regressions indicated that conspecific density, inflorescence count, and plant height affected each pollinator group differently (Table 3). Conspecific density had a positive correlation with *Bombus* spp. visitation in both *P. digitalis* and *M. fistulosa* ($p < 0.001$ for both, Table 3). *Ceratina* spp. were the only pollinator group that visited all three plant species (Fig. 3). However, the co-variates had different effects on it for each plant. Conspecific density was not significant in predicting *Ceratina* spp. visitation in *P. digitalis* or *M. fistulosa* ($p = 0.102$ and 0.822, Table 3), but it was relevant for *E. yuccifolium* ($p = 0.003$, Table 3). Additionally, none of the co-variates impacted *Ceratina* spp. visitation rates in *M. fistulosa,* despite the overall model being significant for the other two plant species. These results may explain some of the weak signals coming from the regression models that considered total pollinator visitation. While conspecific density did not have an effect on total pollinator visitation in *P. digitalis*, it did effect pollinator visitation in both

Bombus spp. and *Ceratina* spp.; visitation among pollinators that did not fall within these two groups were not significant (p = 0.629, Table 3).

Table 1.—Linear regression results detailing the P-values and r^2 values the effects of conspecific density, flower/inflorescence count, height, and distance to forest had on visitation to our focal plant species. Given the distribution of the data, generalized linear models were used to analyze *P. digitalis* and *M. fistulosa*. Nagelkerke pseudo R-squared values were generated to determine the variation explained in these models.

Plant Species	**N**	**Parameters**	**P**	**r^2**
Penstemon digitalis*	150	Conspecific density	0.071	0.538
		Flower count	< 0.001	
		Height	0.006	
		Distance to forest	0.765	
		Overall	< 0.001	
Monarda fistulosa*	51	Conspecific density	0.672	0.918
		Inflorescence count	< 0.001	
		Height	0.222	
		Distance to forest	0.220	
		Overall	< 0.001	
Eryngium yuccifolium**	152	Conspecific density	0.066	0.251
		Inflorescence count	< 0.001	
		Height	0.028	
		Distance to forest	0.54	
		Overall	< 0.001	

*** = Generalized linear model with a Poisson distribution**
**** = Linear model with normalized distribution**

Table 2.—MANOVA results for the effects of conspecific density, flower/inflorescence count, and height on visitation rates based on pollinator identity.

Plant Species	**df**	**Parameters**	**F**	**P**
Penstemon digitalis	3	Conspecific density	3.471	< 0.001
		Flower count	28.425	< 0.001
		Height	1.902	0.132
Monarda fistulosa	3	Conspecific density	12.943	< 0.001
		Inflorescence count	65.485	< 0.001
		Height	0.813	0.494
Eryngium yuccifolium	4	Conspecific density	9.831	< 0.001
		Inflorescence count	7.181	< 0.001
		Height	2.793	0.028

Table 3.—Results from regression models investigating the effects of variables on the visitation of pollinator groups for each plant species. Almost all of these models were statistically significant, with the main differences being which variables were significant. Given the distribution of the data, generalized linear models were used to analyze *P. digitalis* and *M. fistulosa*. Nagelkerke pseudo R-squared values were generated to determine the variation explained in these models.

Plant species	**Pollinator group**	**Parameters**	**P**	**r^2**
Penstemon digitalis***	*Bombus* spp.	Conspecific density	< 0.001	0.331
		Flower count	< 0.001	
		Height	0.244	
		Overall	< 0.001	
	Ceratina spp.	Conspecific density	0.102	0.424
		Flower count	< 0.001	
		Height	0.001	
		Overall	< 0.001	
	Other	Conspecific density	0.629	0.009
		Flower count	0.746	
		Height	0.594	
		Overall	0.856	
Monarda fistulosa*	*Bombus* spp.	Conspecific density	< 0.001	0.749
		Inflorescence count	< 0.001	
		Height	0.951	
		Overall	< 0.001	
	Ceratina spp.	Conspecific density	0.822	0.134
		Inflorescence count	0.828	
		Height	0.088	
		Overall	0.108	
	Other	Conspecific density	0.006	0.838
		Inflorescence count	< 0.001	
		Height	0.409	
		Overall	< 0.001	
Eryngium yuccifolium**	*Ceratina* spp.	Conspecific density	0.003	0.151
		Inflorescence count	0.023	
		Height	0.127	
		Overall	< 0.001	
	Augochlorella spp.	Conspecific density	0.049	0.05
		Inflorescence count	0.053	
		Height	0.045	
		Overall	0.016	
	Coleoptera	Conspecific density	< 0.001	0.099
		Inflorescence count	0.007	
		Height	0.153	
		Overall	< 0.001	
	Other	Conspecific density	0.003	0.183
		Inflorescence count	0.008	
		Height	0.05	
		Overall	< 0.001	

*** = Generalized linear model with a Poisson distribution**
**** = Linear model with normalized distribution**

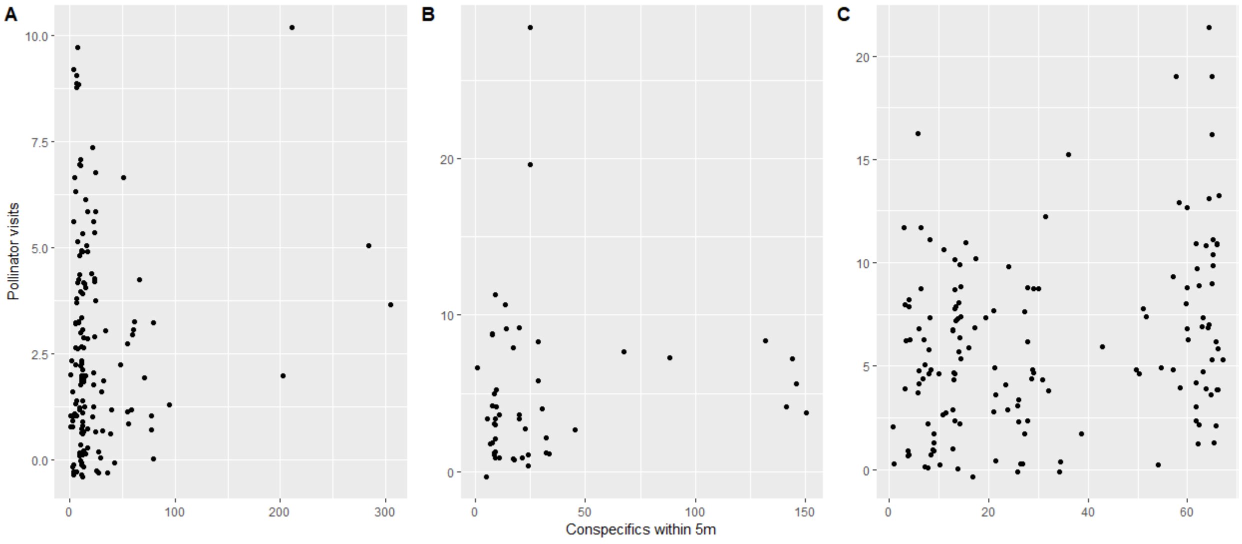

Fig. 2.—Relationship between pollinator visits and conspecific density for (**A**) *P. digitalis*, (**B**) *M. fistulosa*, and (**C**) *E. yuccifolium*. All visiting pollinators were used, and conspecific density had no effect on visitation rates (p > 0.05, Table 1).

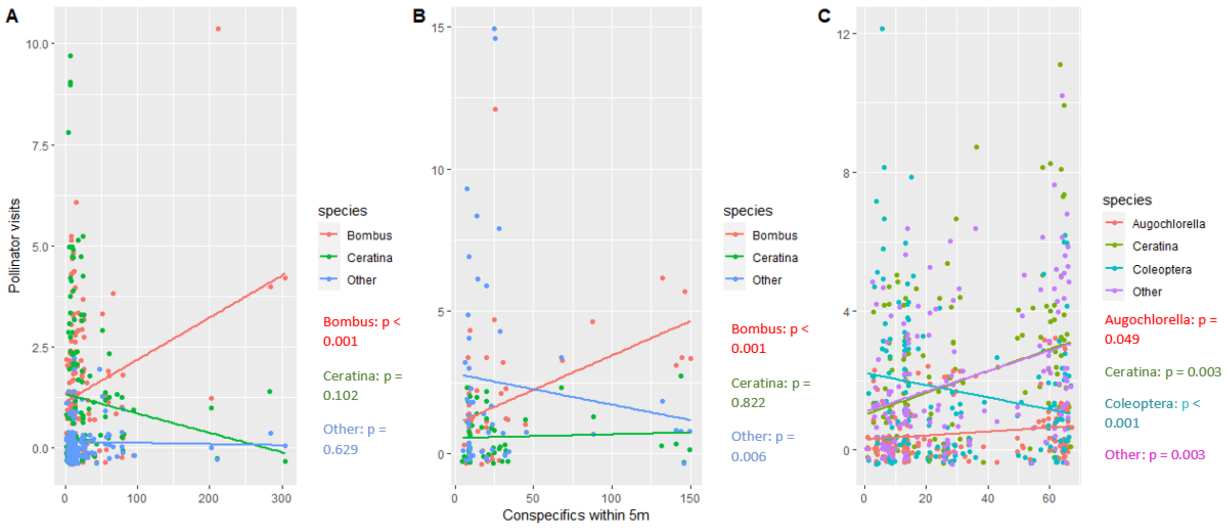

Fig. 3.—Breakdown of pollinator visitation patterns by identity for (**A**) *P. digitalis*, (**B**) *M. fistulosa*, and (**C**) *E. yuccifolium*. MANOVA models investigating the relationships between pollinator identity and conspecific density were all statistically significant (p < 0.001, Table 2).

Seed Set in E. yuccifolium

Seed set was compared to pollinator visitation in *E. yuccifolium* to determine if individual plants that received less visitors were pollen limited. The linear model predicting seed weight from pollinator visits was not significant (p = 0.9), however, many of the pollinator exclusion bags were unsuccessful, breaking the plant and negating the viability of using them. The four controls that were successful did not have statistically lower seed sets than the plants left open, indicating that they either failed in some capacity, or the *E. yuccifolium* was capable of selfing in some way. Despite this, conspecific density did negatively impact seed weight per inflorescence (p = 0.003, Fig. 4). Isolated plants tended to produce higher seed sets than those in larger patches.

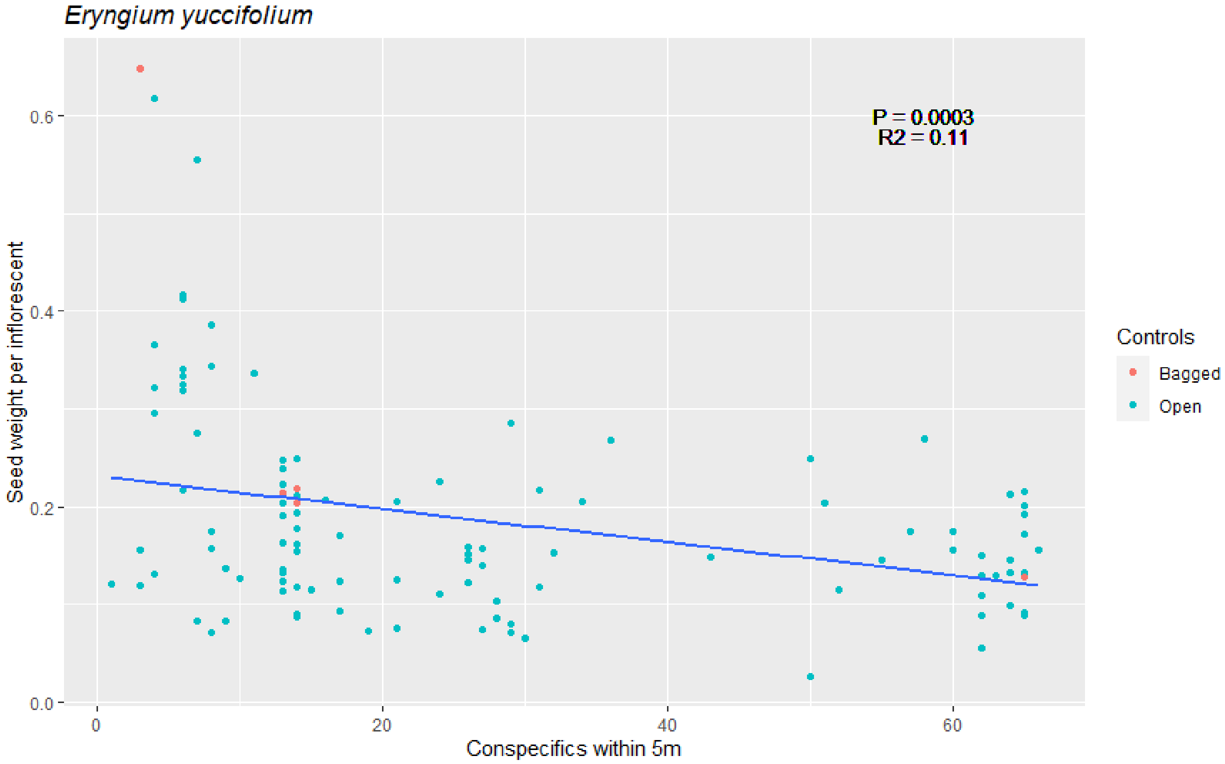

Fig. 4.—Seed weight per inflorescence for each *E. yuccifolium* compared to conspecific density.

Table 4.—Pollinators collected during two-hour sampling efforts for each plant species. All bees were identified to the species level, while any other pollinators were identified at least to family. Only pollinators captured during sampling efforts are included.

	P. digitalis	*M. fistulosa*	*E. yuccifolium*
Anthophora abrupta	✓		
Apis mellifera		✓	
Augochlora pura			✓
Augochlorella aurata	✓	✓	✓
Augochloropsis metallica			✓
Bombus bimaculatus	✓		✓
Bombus griseocolis	✓	✓	✓
Bombus impatiens	✓	✓	✓
Bombus pensylvanicus		✓	
Ceratina calcarata	✓	✓	✓
Ceratina mikmaqi	✓		✓
Coleoptera spp.		✓	✓
Eucera dubitata	✓		
Halictus ligatus			✓
Heriades carinata		✓	✓
Heriades variolosa			✓
Hylaeus mesillae	✓	✓	
Lasioglossum admirandum			✓
Lasioglossum cattallae			✓
Lasioglossum cressonii			✓
Lasioglossum dialictus	✓		
Lasioglossum hitchensi	✓	✓	✓
Lasioglossum imitatum			✓
Lasioglossum versatum	✓	✓	✓
Lasioglossum weemsi			✓
Macroglossum stellatarum		✓	✓
Osmia bucephala	✓		
Osmia conjuncta		✓	
Syrphid spp.	✓	✓	✓
Vespidae spp.		✓	✓
Xylocopa virginica		✓	

Discussion

This study showed how separate plant species within the same restored system can have differing pollinator visitation rates based on the density of conspecifics surrounding these plants. While previous studies have highlighted the impacts conspecific density can have on visitation rates, whether increasing (Silander, 1978; Sih and Baltus, 1987; Kunin, 1993; Kunin, 1997; Ison and Wagenius, 2014) or decreasing pollinator visitation (Wagenius and Lyon, 2010), we found that conspecific density did not have a statistically clear effect on visitation for *P. digitalis, M. fistulosa*, or *E. yuccifolium* (Fig. 2). Our prediction regarding higher density leading to increased pollinator visitation was found to be incorrect when looking at all visiting pollinators. Given that previous studies have found increases or decreases in pollinator visitation based upon higher conspecific density, the results for these plant species fall between those findings. It is possible that conspecific density could have a positive, negative, or even no impact on pollinator visitation depending upon the plant species in question. Research on this topic, therefore, cannot assume that pollinators will select larger patches in every situation. Rather, the picture is significantly more complex, and isolation may not always be impactful to pollinator behavior.

Although there were no clear relationships between patch density and pollinator visitation, the identity of the pollinators visiting individual plants was strongly influenced by conspecific density. Pollinators foraged differently based on flowering patch size, with *Bombus* spp. in particular showing consistency in their foraging preferences. *Bombus* spp. preferentially visited larger patches, which parallels previous research on this pollinator group (Sih and Baltus, 1987; Grindeland, Sletvold, and Ims, 2005). This suggests that they may be opting to be as efficient in their foraging patterns as possible, since visiting a larger patch would reduce their total flight time and energy expenditure. Choosing to visit more isolated flowers would result in more energy being expended for a smaller nectar reward than foraging in a dense patch of flowers. Conversely, other pollinators demonstrated the opposite behavior, instead choosing to visit isolated plants more than dense flowering patches. In *Ceratina* spp., as well as pollinators we categorized as “other”, this may be due to being outcompeted by *Bombus* spp. In this instance, traveling further for nectar rewards could be more advantageous, as flowers in larger patches are more likely to have their nectar taken by *Bombus* bees. These results suggest that, like visitation patterns in general, pollinator groups can have different visitation patterns based on the plant species they are visiting, with different predictor variables impacting those visitation rates.

While conspecific density was not always an important factor in driving pollinator behavior, the physical characteristics of the plants being visited tended to be significant. Taller flowering plants with more flowers or inflorescences tended to attract more pollinators in this study, which is an intuitive finding, given that more flowers can be visited when foraging on a plant that contains many flowers compared to one that has few. This could further reduce the flight time of pollinators, reducing their energy loss. However, plants with more flowers were not visited more per flower, despite having more resources available for pollinators. This is consistent with other studies finding no differences in bumblebee visitation rate per flower in high or low density patches (Klinkhammer and de Jong, 1990). This is because high density patches tend to have more visitors, but fewer visits per flower, while isolated flowers have fewer visitors but more visits per flower (Klinkhammer and de Jong, 1990). Considering that our seed data found isolated flowers tended to have greater seed sets than those in larger patches, it is possible that our isolated flowers were more efficiently pollinated. Conversely, flowers in larger patches may have competed with other flowers for pollinators, and were subsequently not pollinated as effectively.

Future research should consider more than simply isolation and patch density when investigating plant-pollinator interactions. Pollinator behavior is complex, with the layout of flowering communities, individual plant characteristics, and the identity of visiting pollinators having an impact on visitation rates. While these results add to the body of research finding differences among visitation rates based upon pollinator identity (Sih and Baltus, 1987; Grindeland, Sletvold, and Ims, 2005), more research is needed to determine the differences in visitation patterns among pollinator species. The majority of research in this area has focused on honeybee or bumblebee species, with few investigating native bee visitation patterns. Our research has shown that pollinators are not monolithic and that conspecific density can impact native bees differently than bumblebees. Furthermore, our research has shown that plant identity can also impact visitation patterns. *Ceratina* spp. exhibited no preference for flowers that were isolated or in large patches when visiting *P. digitalis* or *M. fistulosa*, but they preferentially visited larger patches of *E. yuccifolium*. Most research in this field has focused on pollinator visitation to one particular flower species, though our research suggests that visitation rates may not just depend upon pollinator identity, but also plant identity.

By understanding the variables that drive pollinator visitation, we can better understand the spatial complexity of plant-pollinator interactions. Pollinators are not a monolith, and we cannot assume they will all behave the same when foraging. The identity of the pollinator is important when determining how variables such as density and plant characteristics will affect their visitation, with some pollinators preferring larger patches, others more isolated plants, and some behaving in more complex ways, with the identity of the plant they are visiting mattering just as much as their own identity.

Future Research

- Research should be conducted on the resource competition taking place in dense *E. yuccifolium* patches. Our data shows that isolated *E. yuccifolium* produced higher seed sets than those in denser patches. Dense patches of *E. yuccifolium* may be competing for nutrients, which could explain why isolated individuals produced more seeds.
- Phosphorescent dye can be utilized to determine how far pollen travels on a visiting pollinator. Data on pollen travel distance could add to this data set by explaining why our plants did not see an effect on visitation from conspecific density, as pollinators may be traveling far enough for our metrics to not be significant.
- This study only collected data on conspecific density, but including all flowering species in density analyses could help to explain our lack of effect on visitation from conspecific density. Low density patches by our metrics may still have had enough neighboring flowers of other species to attract enough pollinators to make the differences between conspecific patches negligible.
- While this study demonstrated the differences in visitation rates based on pollinator identity, the behavioral mechanisms behind these differences are still unknown. Exclusion experiments, where certain pollinator species are removed, in a controlled, greenhouse setting could help determine if smaller, native bees tend to visit isolated flowers to avoid competition with larger bees.

APPENDIX

Table 5.—Descriptive statistics of data collected for each plant species.

Pollinator Visitation

	Total plants used	Total visits	Mean	Visits per minute	Standard Error	Standard Deviation	Variance
P. digitalis	150	414	2.76	0.28	0.40	2.48	6.16
M. fistulosa	51	250	4.90	0.49	0.70	5.01	25.05
E. yuccifolium	152	911	5.99	0.60	0.34	4.20	17.68

Conspecific Density

	Mean	Standard Error	Standard Deviation	Variance
P. digitalis	25.29	3.46	42.38	1795.81
M. fistulosa	30.82	5.64	40.27	1621.43
E. yuccifolium	31.04	1.90	23.44	549.31

Flower/Inflorescence Count

	Mean	Standard Error	Standard Deviation	Variance
P. digitalis	5.83	0.38	4.67	21.77
M. fistulosa	2.84	0.38	2.67	7.13
E. yuccifolium	12.38	0.49	5.98	35.76

Plant Height (cm)

	Mean	Standard Error	Standard Deviation	Variance
P. digitalis	90.23	1.43	17.55	307.85
M. fistulosa	88.04	2.42	17.27	298.17
E. yuccifolium	117.97	2.11	25.97	674.50

Table 6.—Breakdown of pollinator visits to each plant species.

	P. digitalis
Bombus spp.	212
Ceratina spp.	182
Other	21
	M. fistulosa
Bombus spp.	88
Ceratina spp.	28
Other	120
	E. yuccifolium
Augochlorella spp.	72
Ceratina spp.	303
Coleoptera	254
Other	306

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