2020

Bee diversity of three Appalachian shale barren sites

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A thesis submitted in partial fulfillment of the requirements for the degree of Masters of Environmental Science at Virginia Commonwealth University.

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Richmond, Virginia
April 2020

Acknowledgement

I would like to extend my thanks for the support from Virginia Natural Heritage for their enthusiasm and support throughout this project, this study would not have been possible without the personal experience and advice from VANH botanists and zoologists. I would also like to thank the friends and family who spent their weekend assisting me with my sampling trips. Furthermore, I would like to thank Sam Droege, Jason Gibbs, the Arizona Bee Course, Megan Ayers, and Ellison Orcutt who all provided essential help in identifying bees. This project would not have been possible without funding from the Virginia Commonwealth University Center for Environmental Science.

ABSTRACT

Insect pollination is vital to ecosystem function. However, climate change, habitat loss, pesticides, and a variety of other anthropogenic sources are contributing to a decline in pollinator diversity. Fragile small ecosystems with a high composition of specialized plant species that rely on specific pollinators such as Appalachian shale barrens, are especially at risk of losing biodiversity. This study combines the use of active sweep net sampling of endemic shale barren forbs and passive trap methods over the course of a bloom season (April-August) in three barren sites to identify bee community populations and visitation relationships between pollinator species and endemic flowers. From all samples, 72 species of bees were identified. Both Shannon’s Diversity Index and a rarefaction analysis of Month x Site indicate May is a time of highest species diversity for bees. Among individuals caught visiting flowers, June was indicated as a time of highest flower visitations. A pollinator network was created to identify unique relationships between pollinators and flowers, providing information on species of particular value to those systems for future conservation purposes. Species records from this survey contribute to expanding the currently limited data on bee species range, life history, and flower associations.

INTRODUCTION

Insect pollination is vital to ecosystem function, up to 67% of flora are dependent on pollinator species for reproduction (Tepedino 1979) and pollination from fauna is considered to be a major driving force of evolution in flowering plants (Kevan, 1975). Floral traits have been traditionally recognized as a reflection of the pollinator type they rely on (Fenster *et al.*, 2004), and abundant pollinator variation leads to diverse flora populations (Ghazoul 2006).

However, climate change, habitat loss, pesticides, and a variety of other anthropogenic sources are contributing to a decline in pollinator diversity (Buchmann and Nabhan 1996; Kearns *et al.* 1998; Kevan 1975). Along with declines in pollinator populations, plant species reliant on the pollinators have also declined, creating a disturbing loss in ecosystem diversity (Biesmeijer *et al.* 2006). Fragile small ecosystems with a high composition of specialized plant species may especially be most at risk.

Appalachian shale barrens are small community patches defined by their location on steep open south-facing xeric slopes with thick shale strata and unique plant community (Keener 1983). These communities are listed as globally uncommon and range from southern Pennsylvania to western Virginia (Fleming *et al.* 2020). Compared to the surrounding pine and hardwood forest, shale barren openings are poorly vegetated with patches of bare rock faces.

The high temperatures, low moisture, and loose rock strata make shale barrens a difficult place for plants to grow (Keener 1983). As such, plant composition often consists of a few stunted tree species and a wide variety of herbaceous plants including a number of rare species adapted to these conditions, such as the federally listed *Boechera serotina* and *Trifolium virginicum.* These communities also contain several rare animals, such as the butterflies *Pyrgus* *wyandot* and *Euchloe olympia*, that rely on the endemic flora (Weakley *et al.* 2012). *Pyrgus wyandot*, for example, is a skipper whose larvae develop only on *Potentilla canadensis*.

However, these rare communities are threatened by human development, spreading invasive species, and overgrowth caused by fire regime suppression (Tyndall 2015). The development of logging roads and agriculture provides corridors for the establishment of invasive species such as spotted knapweed, crown-vetch, and Japanese honeysuckle which create shade for the sun-sensitive endemic flora (Maryland Department of Resources). Additionally, efforts to control an invasive insect have caused harm to vulnerable shale barren species. In the early 1990s, *Pyrgus wyandot* populations were severely damaged by Dimilin spray to control gypsy moth populations and they have since been placed on the endangered species list (Nott 2006).

Floral diversity and abundance are important drivers of bee communities, particularly in open habitats, such as shale barrens, that occur within wooded landscapes. (Potts *et al.* 2005). A previous bee diversity survey of shale barrens performed across several years in Maryland using malaise traps found several rare species for the state, such as a *Vaccinium* specialist *Melitta eickworti* (referred to as *Melitta americana* in the paper) (Kalhorn *et al.* 2003). The study also found that compared to the woodlands surrounding the shale barren, higher bee species diversity occurred within the barren openings as a result of the presence of many food plants. However, these sampling efforts lack data on which plants bees were visiting for food which would need to be collected through active net sampling methods.

Concerns over native bee community biodiversity losses require surveys to monitor population levels (Spring *et al.* 2017). It is acknowledged that declines in pollinator diversity are difficult to study due to lack of prior population knowledge (Stokstad, 2006), making current research essential for future conservation work. This study aims to provide a descriptive baseline of bee populations in Appalachian shale barrens, as they are highly specialized and fragile ecosystems, and to observe unique connections between flora and their bee visitors.

METHODS

Study Area

Sites were on the steep southern slope of three ridges along Fortney Branch Road in Alleghany County, Virginia - located in George-Washington Jefferson National Forests (Figure 1). Small seasonal tributary streams undercut each site and fed into the southern reservoir of Lake Moomaw. Sites were less than .45 km away from each other, between 3-5 acres, and at an elevation between 1800-1900 ft above sea level (Figure 1).

These sites were chosen because of their proximity to each other and a record of prior botanical surveys from the Department of Conservation and Recreation (DCR). Prior DCR survey data from 1996-2012 observed *Boechera serotina, Eriogonum allenii, Trifolium virginicum, Clematis albicoma*, and several other endemic herbs. The only prior recorded invasive species in the sites were an observation of *Verbascum thapsus* in the southern site in 2012 - this species was not observed during our study. Tree species within the barren community were *Juniperus virginiana, Quercus montana, Carya glabra, and Carex pensylvanica*. Sites are classified as Central Appalachian calcareous shale barrens with a G2S2 element rank through the DCR.

The shale opening of the most northern site (Site 1) was clear and open (Figure 5), with very little undergrowth and characterized by stunted or dead oaks and a significant covering of Reindeer moss. The two southern sites (Site 2 and 3) were more overgrown with bare open sites reduced. It is possible the sites have become overgrown since prior DCR survey, but endemic herbs were still observed and present (Figure 6, 7). The majority of endemic flora was observed in the southern site on a rocky open outcrop near the edge of the shale barren patch.

Data Collection and Analysis

Sampling took place from April to August 2019, in intervals of two weeks, and used a combination of both active and passive sampling approaches. Surveys occurred over a two day period, where each site was visited to reset traps and hand-collect from flowers for two hour periods. The same process took place on the second day, but the time of day each site was visited was reversed in order to account for time sensitivity in bee activity.

Bees were collected by hand and sweep netted when they were seen making contact with a flower. They were killed using ethyl acetate and then placed in collection tubes, separated by cotton balls in order to prevent pollen from mixing between specimens. Pollen was preserved in order to identify and be used for potential future pollen analyses. Blue vanes were placed in each site at the spot with the highest density of flora and were left between visits filled with propylene glycol (Droege *et al.* 2016). Blue vanes and a set of 10 blue and yellow bee bowls were filled with soapy water and collected after 24 hours during the two-day visiting periods.

The passive trap caught bees were cleaned and processed in the lab using methods from Sam Droege (Droege *et al.* 2016). Hand caught bees were not cleaned in order to preserve pollen loads. All bees were identified using discoverlife.org guides and assistance from Sam Droege, of USGS Patuxent Wildlife Lab. Flowers were identified to the lowest taxonomic level using guides in the Flora of Virginia and confirmed by Chris Ludwig.

Data were analyzed using the RStudio *vegan* package, which offers a wide variety of diversity measurement tools for descriptive ecology (Oksanen *et al.* 2019). Shannon's diversity index was used to compare biodiversity measures between each site, and Rarefaction curves were generated to account for the sampling effort to aid in comparison across sites and sampling intervals. In addition to diversity, an analysis of similarity was performed to test sampling differences between months and sites.

In order to identify unique connections between potential pollinators and the flora they visited, bi-partate visitation networks were generated using the *econullnetr* R package (Vaughan *et al.* 2018). Bees caught through sweep net with recorded flower interactions were used in the network creation. One side of the network represents plant species while the other half represents species of bees that were caught making contact with flowers. Lines between the two sides represent an interaction of those species. These visitation network models were compared to a null model of plant/bee interactions generated in order to identify significant connections between bees and plants that occur stronger than a random expectation. Strong one way relationships wherein either a bee visits only one flower, or a flower is visited by only one bee, were also identified through this approach.

RESULTS

Between all three sites, 1024 specimens, composed of 72 species of bees from 20 genera were collected (Table 1). The most common bee sampled was *Augochlora pura*, a generalist in the Halictidae family. The trap method with the most specimens caught was blue vane (595) followed by sweep net (353). The number of specimens caught across the sites was unequal, with over half of the samples (619 bees) caught at Site 3. This is largely due to a single blue vane trap which caught 362 specimens—almost all of which were *Augochlorella aurata* or *Augochlora pura*—which is unusual for trapping and was treated as an outlier. Removing this leaves sites roughly equal to each other. The contents of this trap were removed for subsequent analyses.

Bee biodiversity was quantified between each site and month using Shannon's Diversity Index. Site 1 in May had the highest diversity level (S = 3.14), while diversity across all three sites declines sharply afterwards (Figure 3). A rarefaction curve was also generated showing similar results. Rarefaction is a way to assess species richness by level of sampling effort in order to determine whether more sampling is needed for an accurate assessment of species richness (Figure 2). Rarefaction curves measuring the number of new species collected by each sample within monthly data, and samples in month x site, never reach an asymptote and indicate further species are unsampled within seasons and site (Figure 4a, Figure 4b). An analysis of similarity using a Bray-curtis dissimilarity matrix between months shows species composition was significantly different to each other (R=.716, p=0.001) (Figure 15). The greatest difference in species composition was between April and August, while August and July were closest (Table 2). There was no significant difference in species structure between sites (R=-0.116, p=0.84; Figure 16).

The bi-partate bee-flower visitation networks using R package *econullnetr* shows unique relationships between bees and their associated flowers. Lines indicate a visitation, and width of lines indicate the abundance. Visitation data was compared to a null model to determine significant interactions. Networks were broken down by month to account for phenological seasonal differences influencing visitation levels. From this, *Andrena gardineri* stands out as solely visiting *Packera antenariifolia,* which had visitors from several other species (Figure 8, 10). *Augochlora aurata,* a common generalist species, was found higher than expected on *Asclepias tuberosa* (Figure 9).

Species in the *Ceratina* genus (*C. strenua and C. calcarata)* had a strong relationship with *Hieracium traillii* during the month of May (Figure 11), and *C. strenua* expanded to other plants when *H. traillii* became unavailable while *C. calcarata* no longer appeared caught (Fig 12, Fig 13). From the flower side, there is a one-to-one relationship between *Fabaceae sp.* and *Anthidiellum* in July (Figure 13). Overall, flowers in the family *Fabaceae* were visited by bee species in the family *Megachile* (Figure 8). Furthermore, *Asclepias tuberosa* appears to be the most common flower visited overall from a wide variety of bee species in June, but then drops out of bloom in July (Figure 12, Figure 13). No significant relationships were observed between *Boechera serotina* and its two visitors, *Augochlorella aurata* and *Megachile mendica* (Figure 13). Nor were visitations by *Osmia pumila* on *Trifolium virginicum* higher than expected under a null model (Figure 11).

DISCUSSION

This study expands our current knowledge of bee species present in Virginia and their potential range and life history. These results will contribute to current efforts to track Virginia bee populations, such as efforts by the Virginia DCR Inventory compiling a state species list. The combined use of active and passive trapping collects a range of species that would otherwise be missed by one sampling type. As such, we are able to update limited prior knowledge of shale barren pollinator communities. Compared with the Kalhourne *et al.* (2003) study on shale barren bees, we add 57 additional bee species collected from this ecosystem along with additional flower host information and season emergence. This study has the benefit of using updated bee taxonomy to be able to identify specimens to species that may not have had descriptions in 2003 - such as many in the *Lasioglossum* genus.

Some particularly uncommon bees caught during this study include *Osmia felti*, which is considered a rare bee associated with barren habitats, and its first Virginia records are from 2018 in Rockingham county, VA. Similarly, we caught eight *Pseudopanurgus virginicus* from *Houstonia sp.,* which only has a single Virginia record from 2018 and has historically been associated with *Houstonia sp.* (Ascher *et al*. 2009). Our study also caught 16 *Lasioglossum fattigi*, a ground nesting generalist, which is considered uncommon to collect (Onuferko *et al.* 2015). These small bees often go unobserved and under-collected. Parasitic bee life history is also particularly difficult to track, with their host species usually unknown. Collection of *Nomada seneciophilia* is rare, but hypothesized to be a parasite on *Andrena gardeneri.* Collection of both species from this study seems to support this but further research would be required to confirm.

Life history knowledge of bee species is limited, with few surveys able to collect which habitat they rely on or plant species they visit for pollen and nectar. This study expands what we know, especially for uncommon species that are rarely collected. Understanding which bees may be pollinating shale barren plants is helpful for maintaining rare and endangered plant population health. For *Boechera serotina*, rarity of plant specific pollinators is listed as one of the major threats to populations, as inability to cross-pollinate would eventually lead to inbreeding depression (Nott 2006). Bees have been observed to visit these plants, but specific species were not identified (Nott 2006). We observed *Augochlorella aurata* and *Megachile mendica* as visitors, both common species.

Increased overgrowth at two of the three sites indicates a potential threat to shale barren ecosystems from forest management practices such as fire suppression methods in the 20th century. This practice has allowed hardwood trees to form a shaded canopy in barren openings. Prior DCR records at Lake Moomaw observed evidence of past fire in the three sites, and studies from the region indicate historic records of frequent fire every 5-17 years until 1930 (Aldrich *et al.* 2010). A burn study of shale barren plots in Maryland found that fire increased the diversity and species richness of flowers, particularly benefitting endemic ones like *Trifolium virginica* which rely on bare soil and direct sunlight. Furthermore, the larval host plant for *Pyrgus wyandot*, *Potentilla canadensis*, increased in the forest ecotone around the barrens (Tyndall 2015). Increasing these flowers would also benefit bee populations that rely on them.

Relationships observed through the visitation network allows us to identify several potential valuable pollinator-plant relationships that give us insight to the function of bees within the shale barren system. For example, *Packera anteniifolia* seems to be an essential flower for *Andrena gardineri*, an early spring bee, but the plant species does not rely on *A. gardineri* as its sole pollinator. Likewise, *Ceratina strenua* and *C. calcarata* exhibit a preference for *Hieracium traillii* but *C. strenua* is flexible and does not rely on it, its visitation season within the shale-barren extending throughout summer. These relationships may be strongly influenced by the abundance of a flower in each plot as well, as *Asclepias tuberosa* was the most abundant and also the most visited.

The observed interaction between bees and their associated plants are restricted by lack of pollen information. These relationships can only be described as "visitations" with limited speculation that they are pollination events. Furthermore, limited assumptions can be made as a result of restricted sample size. Especially for endangered plants, more observations between a bee species and their associated flowers need to be made before they can be considered significant pollinators. However, future collaborative work can expand our network to identify pollination relationships through genetic pollen analyses on the pollen loads of specimens caught.

Rarefaction curves generated indicate that a sampling threshold was never reached, and new species were continuing to be caught with each sample (Figure 3). Further multi-year bee studies on these systems are likely to yield additional new, and increasingly uncommon, species. This study was restrained by being a single-year study, weather conditions, and unexpected sampling disturbances (such as bears) that may skew data.

This study sets up essential information needed for future work in these systems. Shale barrens as isolated fragmented patches with unique evolutionary histories provide an opportunity for the study of pollen dispersal between island patches. In order to do so, basic knowledge of the pollinator species present in sites and their general visitation patterns are required. This study provides insight into a vital function of a rare ecosystem and may help conservation managers target critical flora and fauna to protect. The collection of rarely observed species indicates there are many more rare insects to be found through further sampling.

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TABLES AND FIGURES

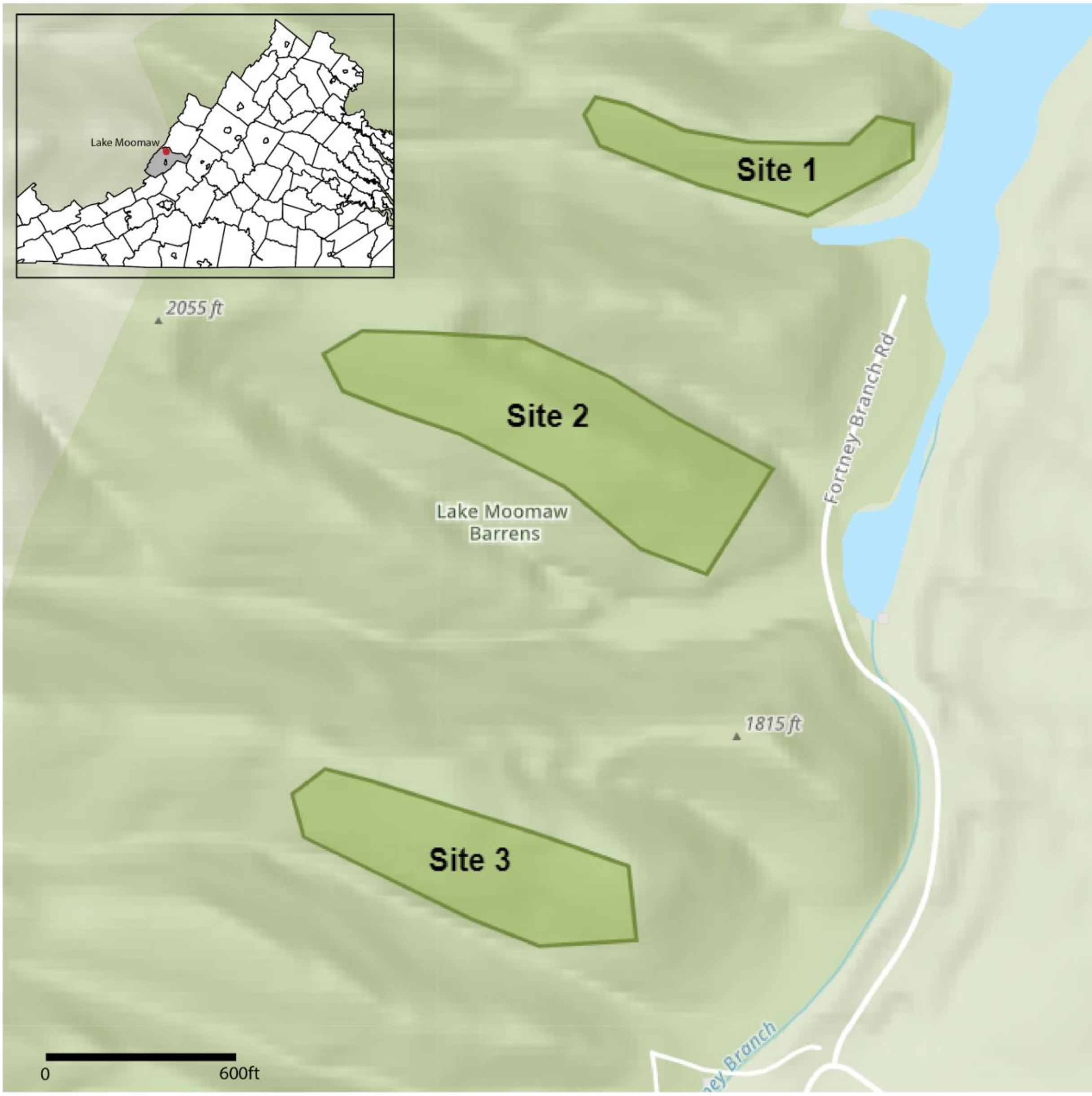

Fig 1. Study sites along Fortney Branch Road at Lake Moomaw in Alleghany County, VA.

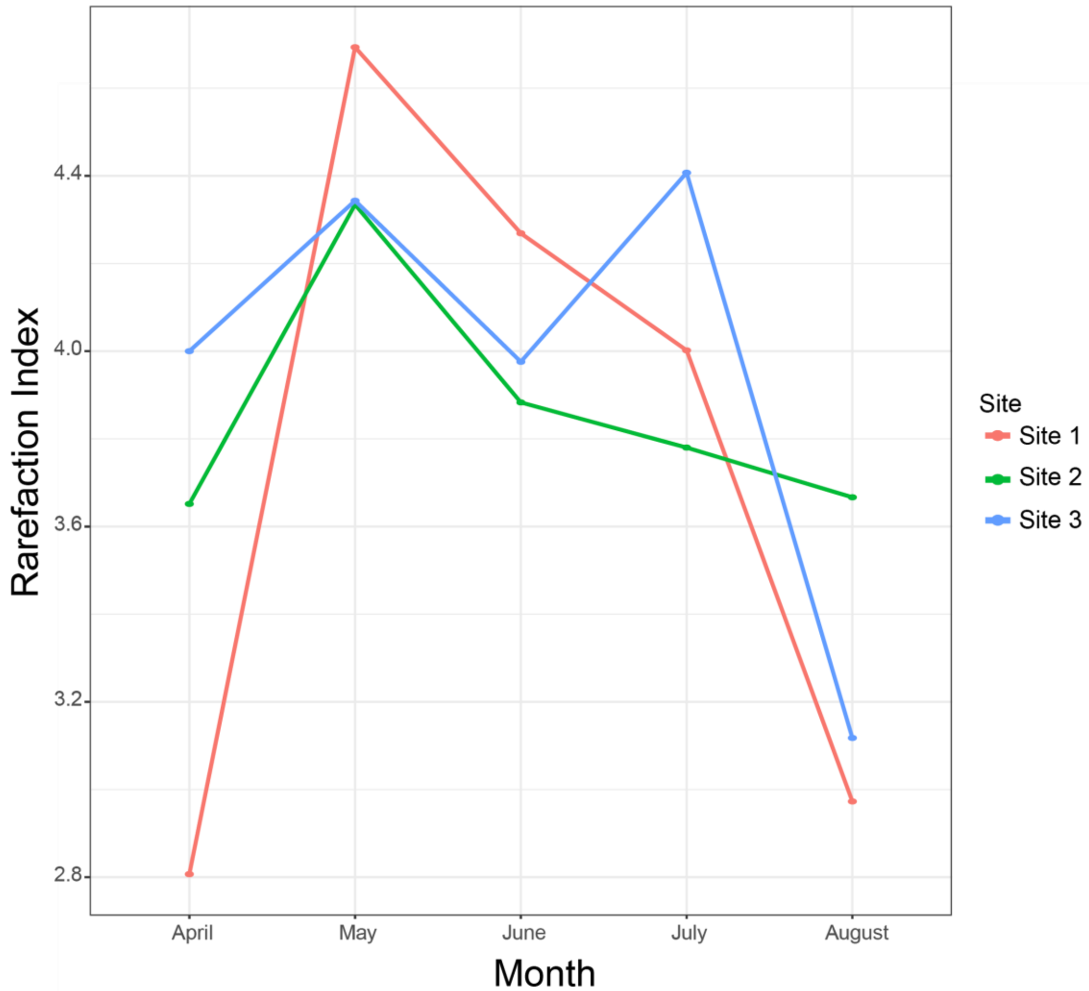

Figure 2: Rarefaction of bee species diversity for the three Virginia shale barren sampling sites by month.

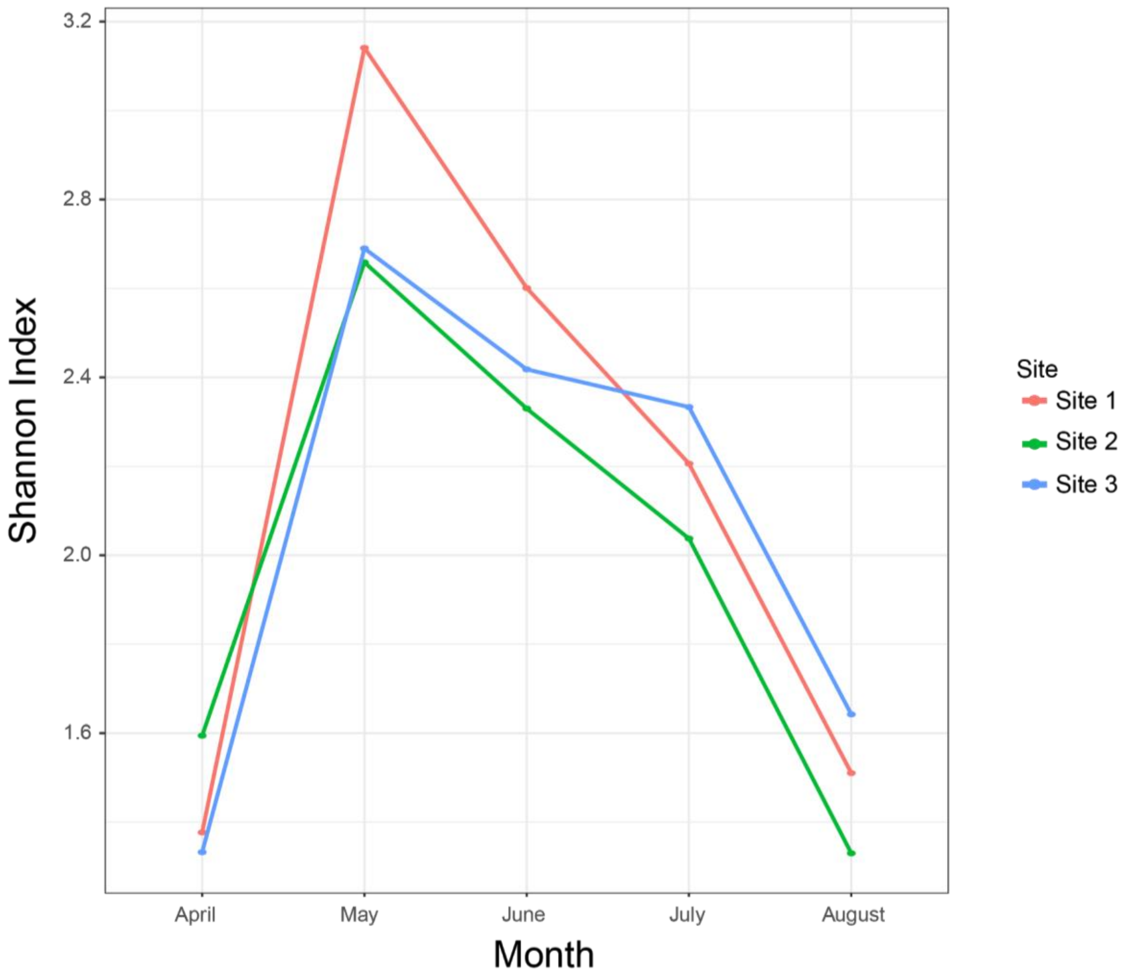

Figure 3. Shannon's Diversity Index across site and month.

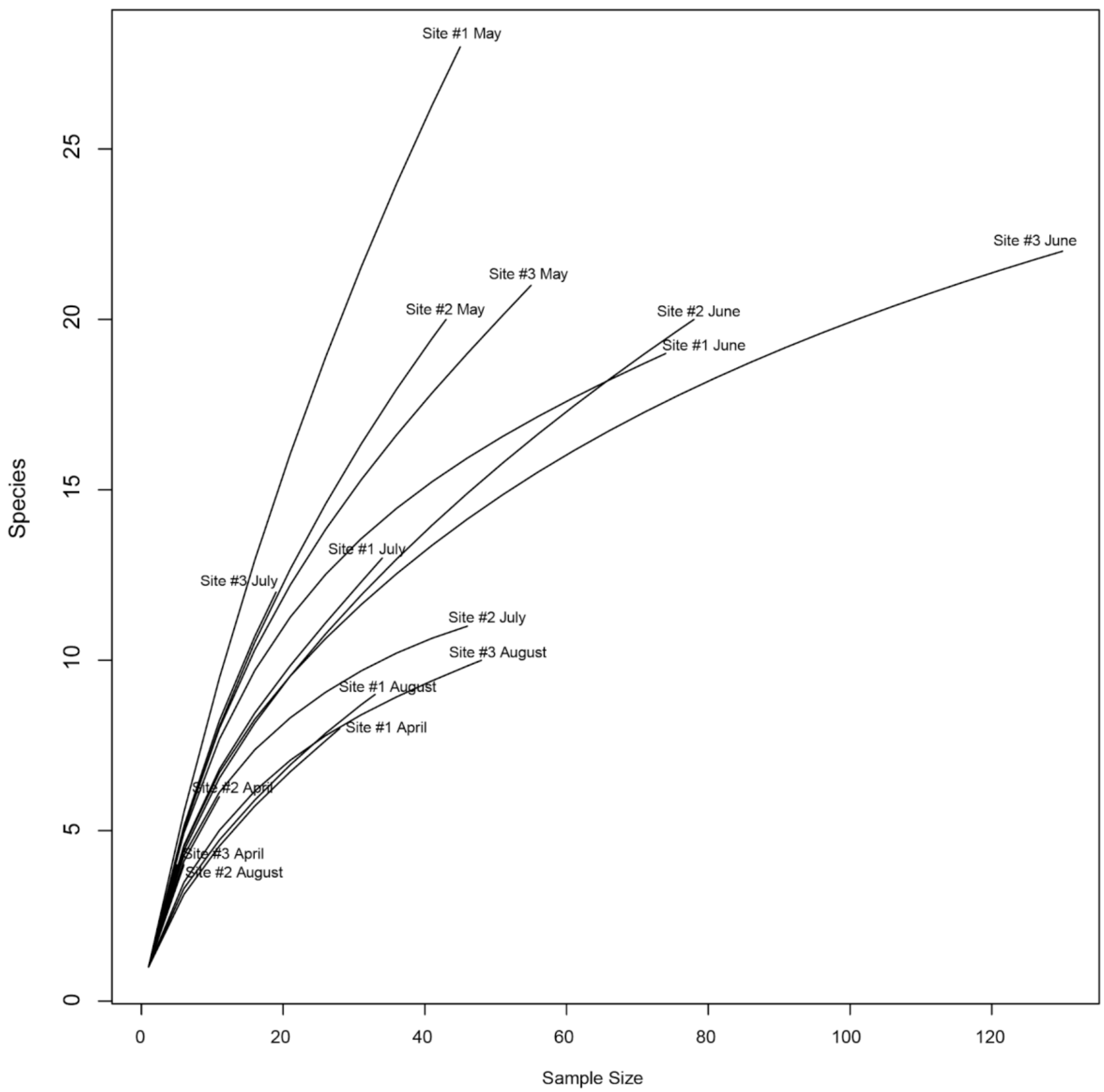

Figure 4a. Rarefaction curve of new species collected for each sample. Outlier data was removed.

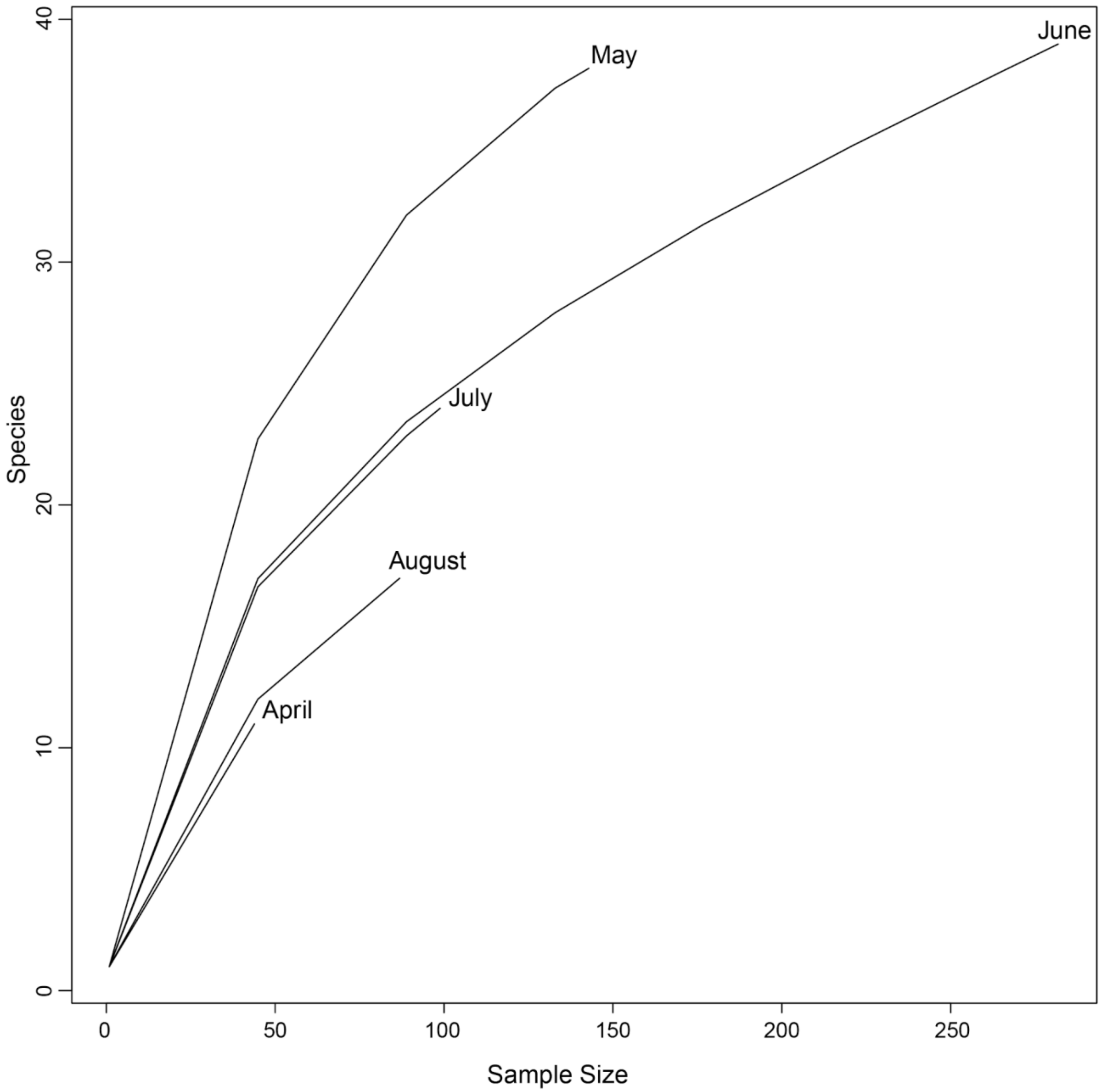

Figure 4b. Rarefaction curve of new species collected for each month. Outliers are removed.

Figure 5: The northern shale barren site denoted as Site 1 in the text.

Figure 6. The central site, denoted as Site 2 in the text, showing various grasses and the spread of blue and yellow bee bowls used for passive trapping. Photo credit: Rodney Dyer

Figure 7: The Southern Shale Barren site, denoted as Site 3 in the text. Photo credit: Rodney Dyer

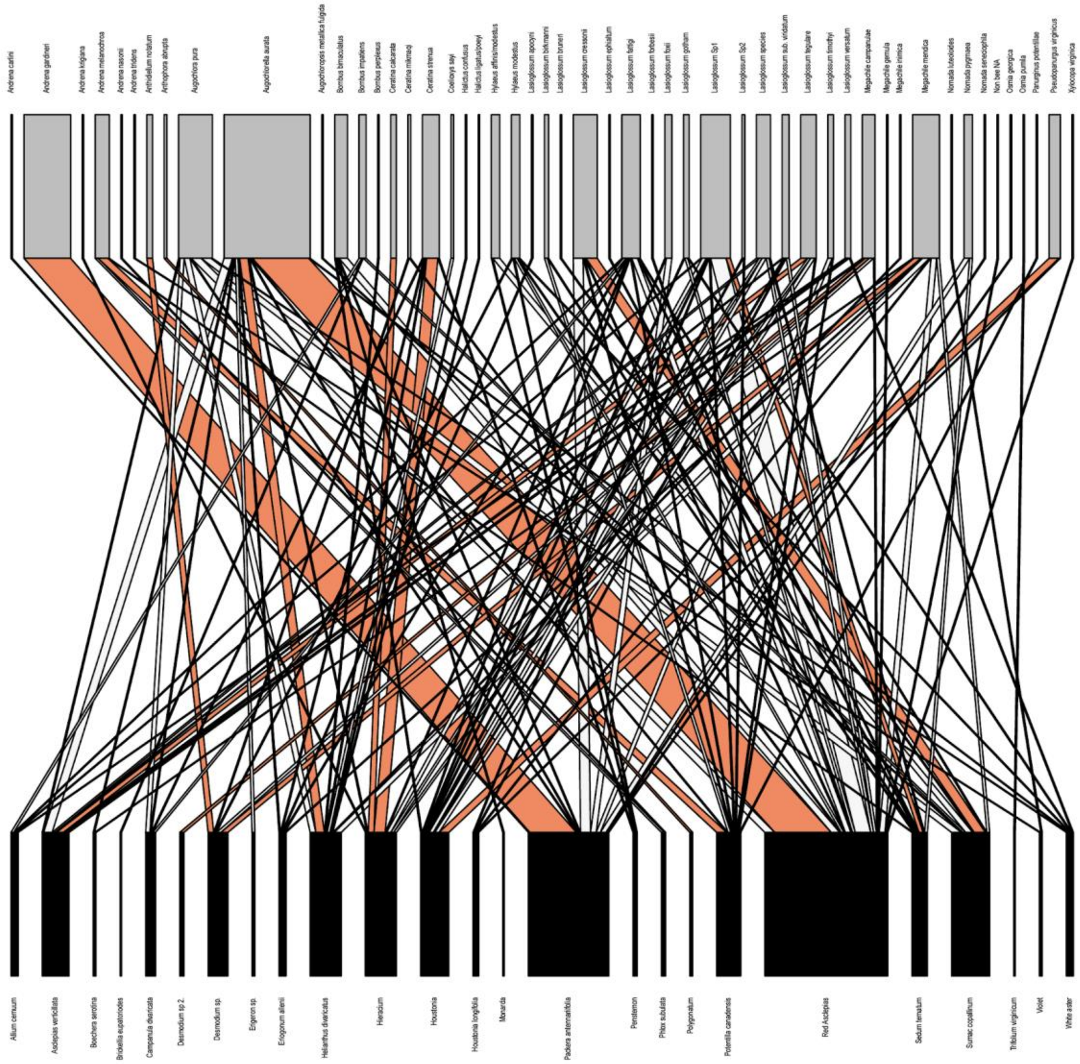

Figure 8. A bipartite visitation network showing interactions between bees species on the top bar and flower species on the lower. Line width indicates abundance, blue lines indicate visitation was less than expected under a null model, and red lines indicate visitation was higher than expected under a null model. The network shows overall interactions for all months.

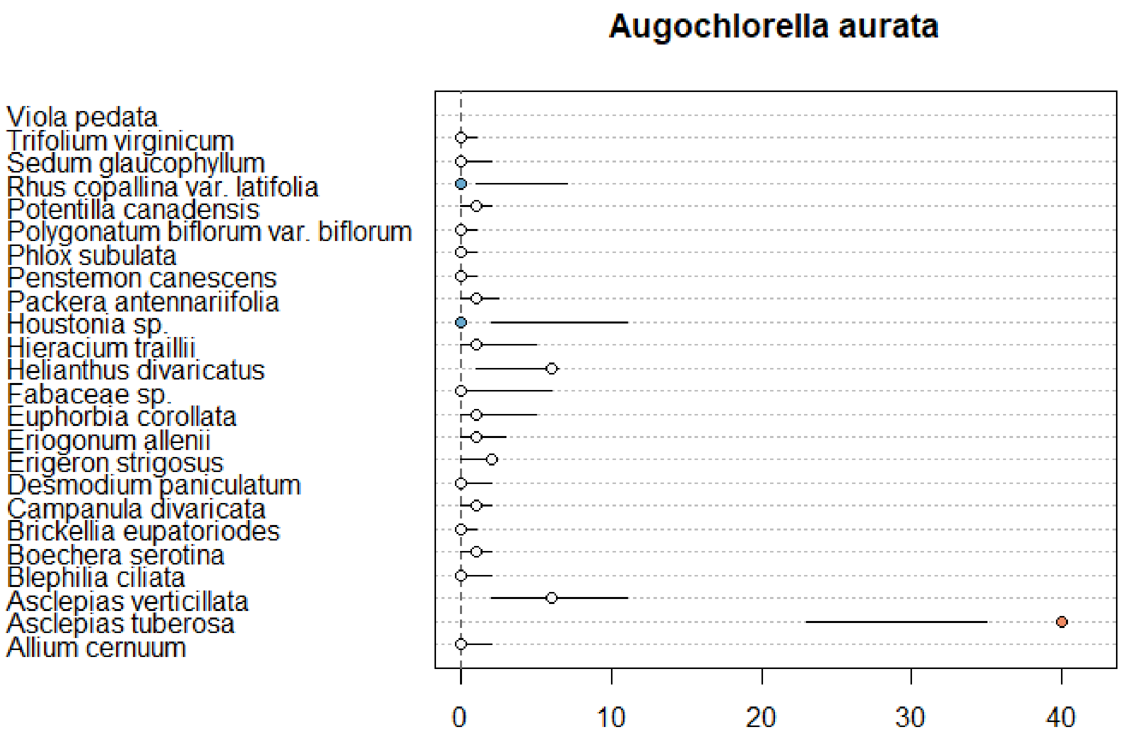

Figure 9. *Augochlorella aurata* had a higher observed association with *Asclepias tuberosa* than expected under a null model across the overall season. Horizontal lines represent the confidence envelope under a null model, while dots represent the actual observed visitation frequency. Red indicates a significantly higher difference compared to the null model, while blue indicates a significantly lower difference.

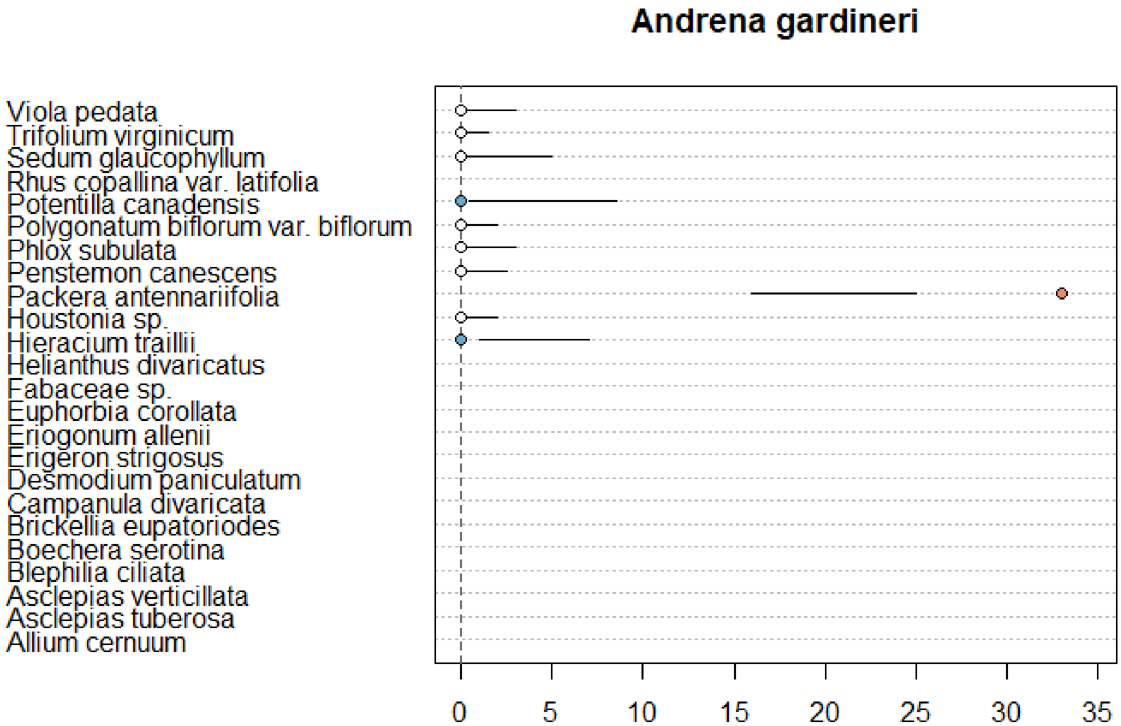

Figure 10. *Andrena gardineri* had higher observed association on *Packera antennariifolia* than predicted by the null model. *A. gardineri* solely visited *P. antennariifolia* across the season.

Figure 11. Visitation network for May. Significantly higher than expected associations are marked in red.

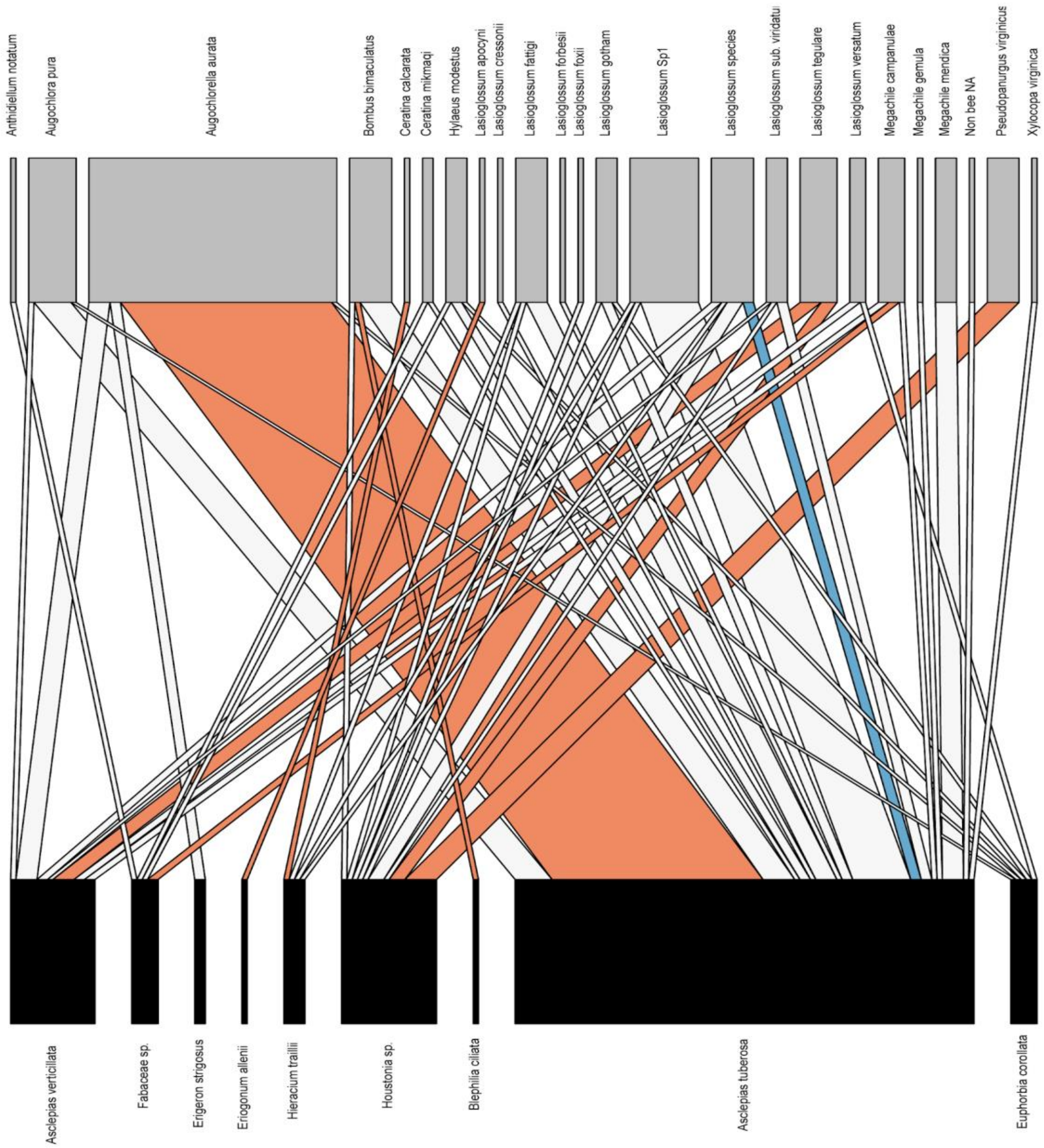

Figure 12: Visitation network for June. Significantly higher than expected associations are marked in red, and significantly lower than expected are marked in blue.

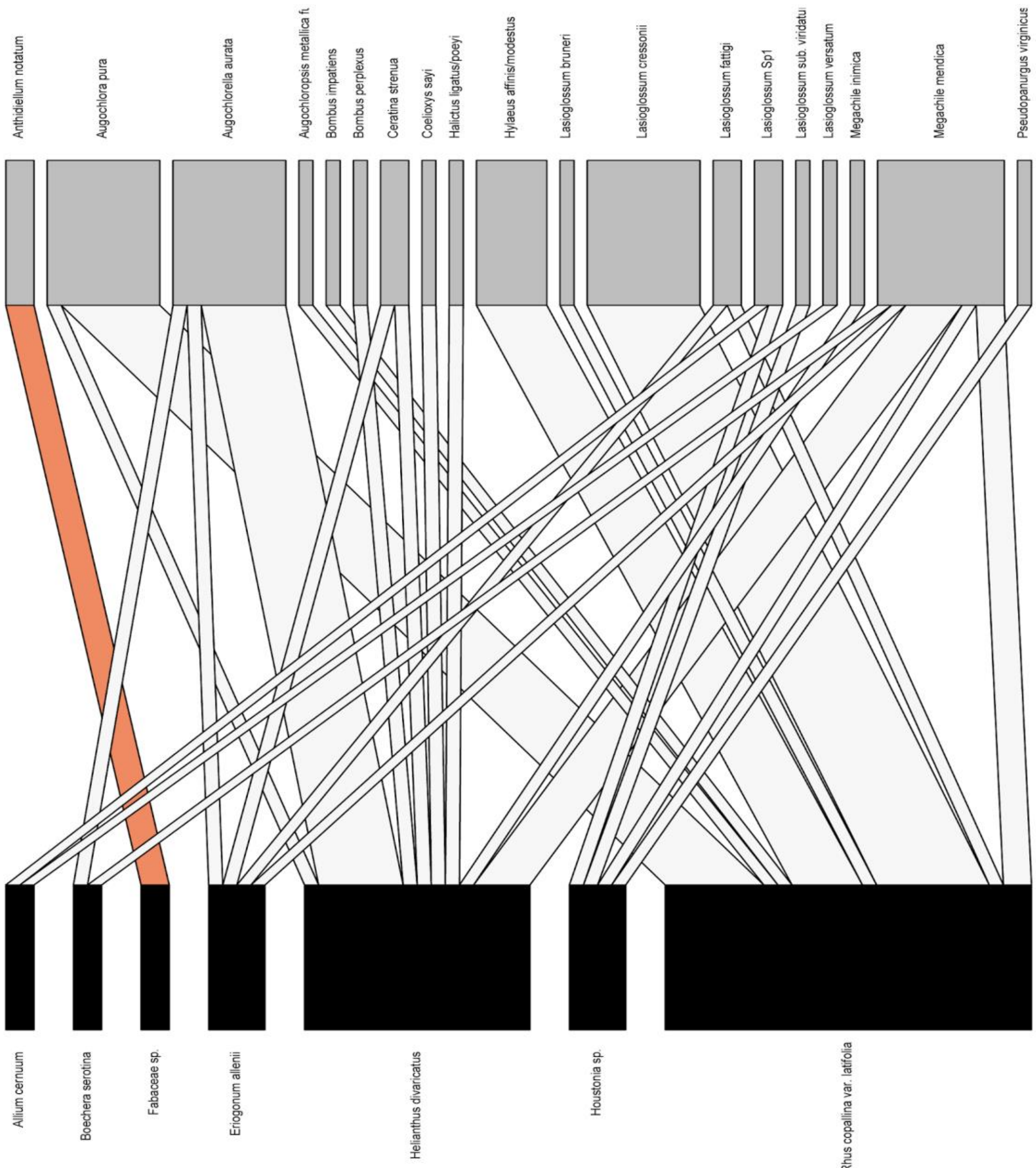

Figure 13. Visitation network for July. Significantly higher than expected associations are marked in red.

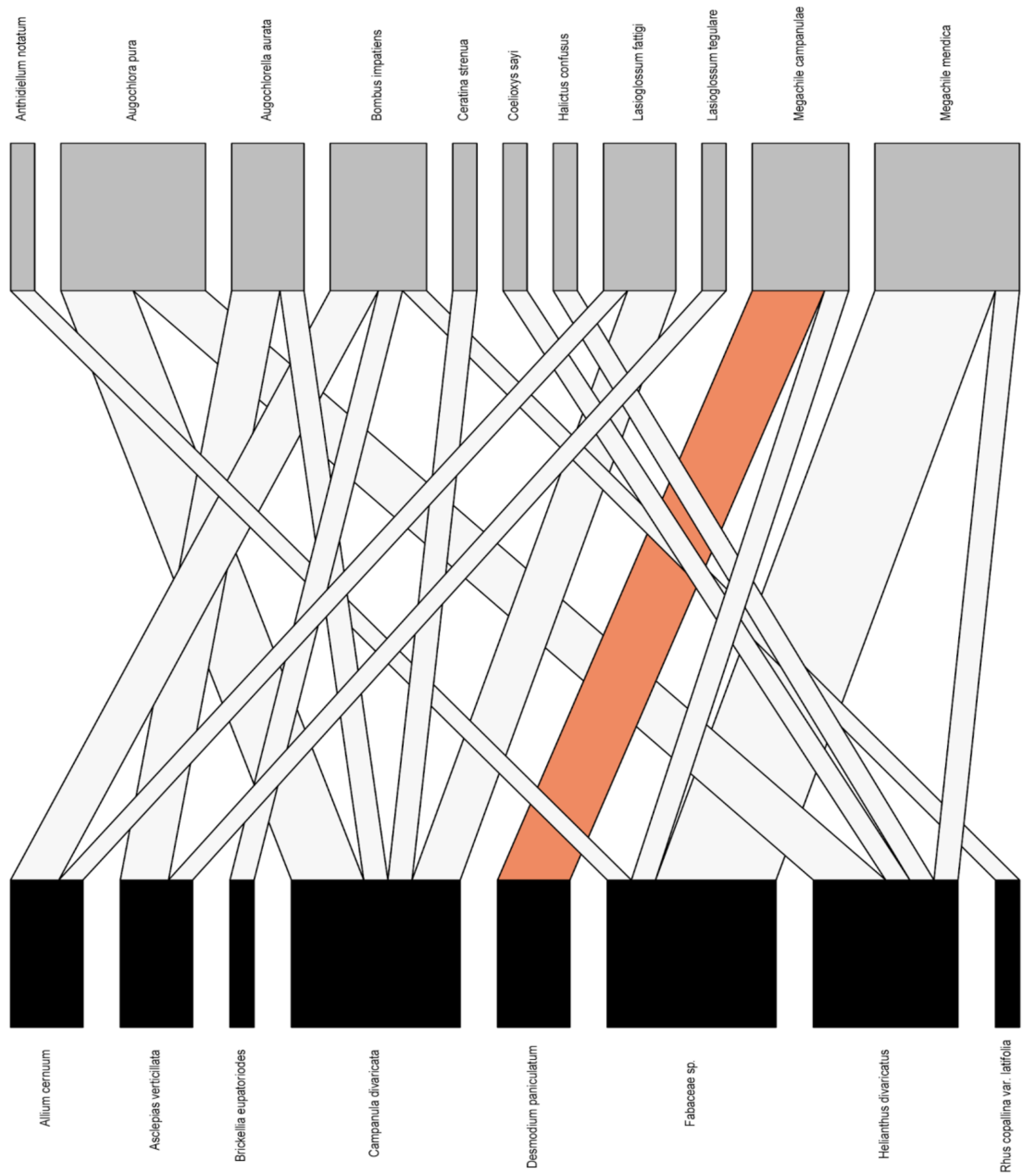

Figure 14. Visitation network for August. Significantly higher than expected associations are marked in red.

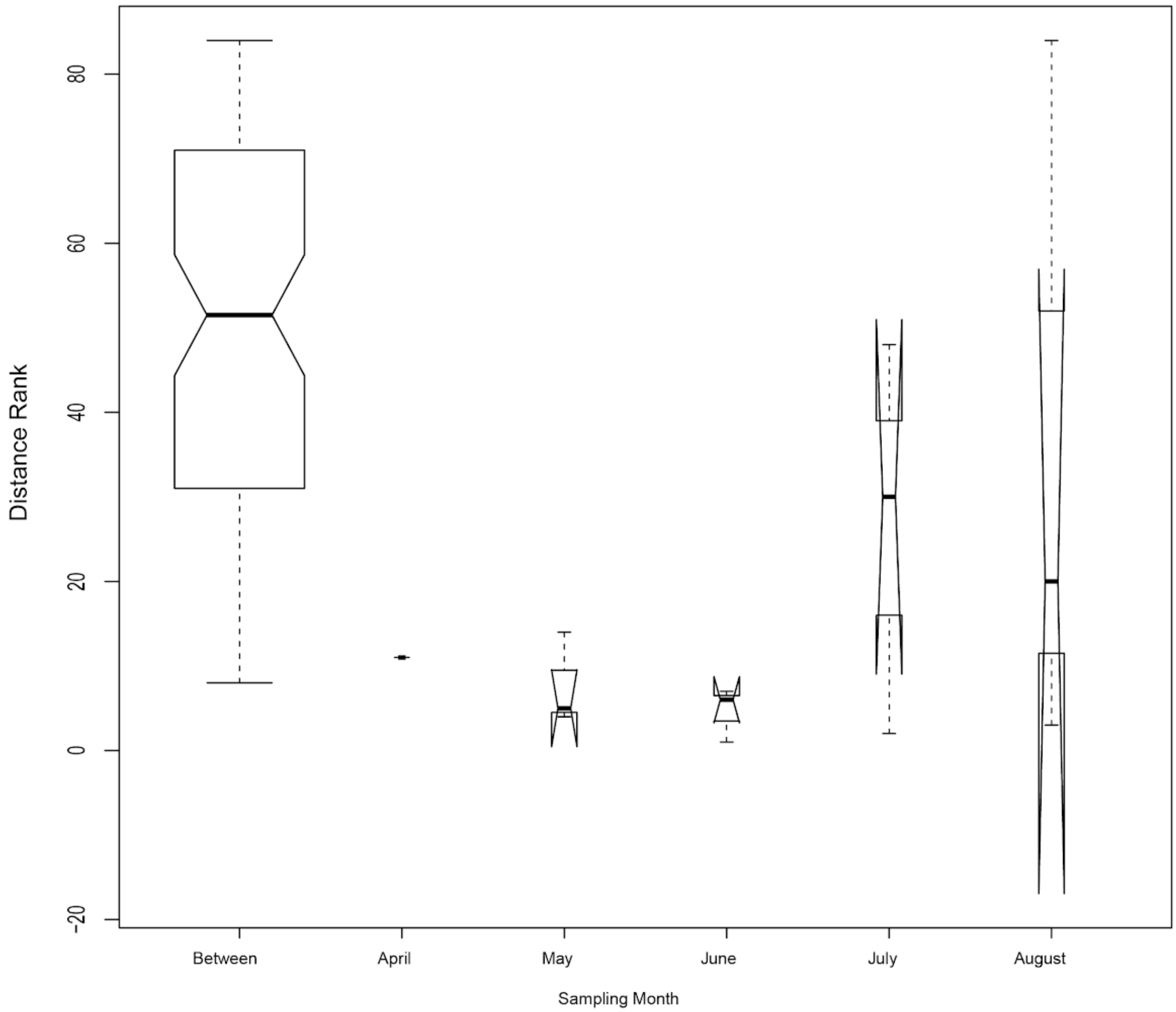

Figure 15: Boxplot of analysis of similarity results between sampling months. Observed correlation was positive and significant (R=0.716, P=0.001).

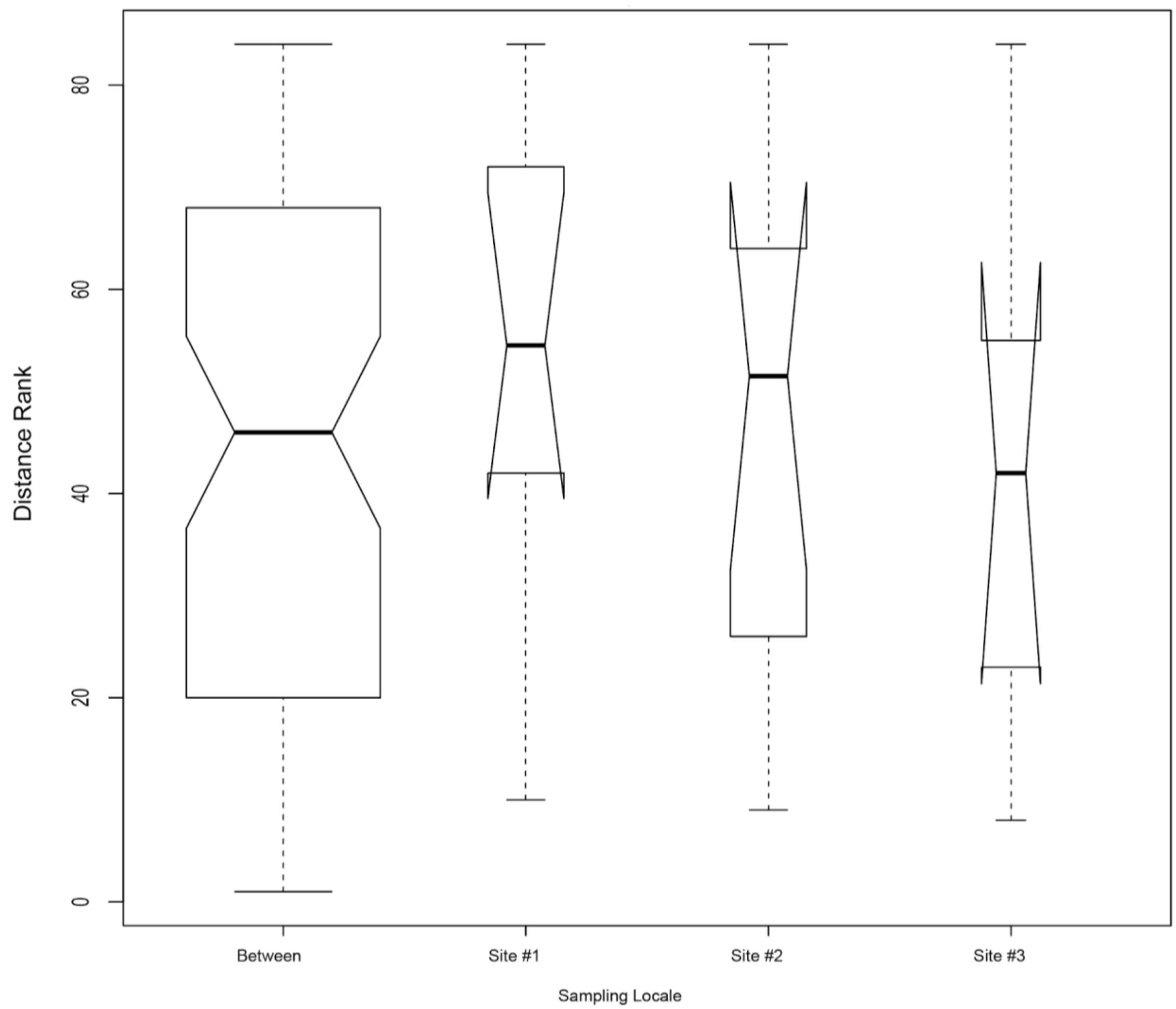

Figure 16. Boxplot of analysis of similarity results between sampling sites. Observed correlation was slightly negative but not significant (R=-0.116, P=0.816).

Table 1. A list of species caught across all methods and sorted by family, the amount caught, what flower they were caught on, and the month they were found. An asterisk (*) indicates an introduced bee species as defined by usgs.gov. Highlights in red indicate a species caught only on one species of flower. Blue text indicates flowers only visited by one species of bee.

Family	**Species**	**#**	**Flower Sweep**	**Month**
Andrena	*Andrena carlini*	3	*Packera antennariifolia*	April
	A. distans	3		
	A. gardineri	33	*Packera antennariifolia*	April-May
	A. krigiana	1	*Hieracium traillii*	May
	A. melanochroa	10	*Phlox subulata, Potentilla canadensis, Sedum glaucophyllum*	May
	A. nasonii	3	*Phlox subulata*	May
	A. tridens	1	*Viola pedata*	April
	*A. wilkella**	1		
Apidae	*Anthophora abrupta*	6	*Polygonatum biflorum var. biflorum*	May
	Bombus bimaculatus	54	*Houstonia sp., Blephilia ciliata, Packera antennariifolia, Asclepias tuberosa*	April, June
	Bombus impatiens	78	*Allium cernuum, Brickellia eupatoriodes, Rhus copallina var. latifolia*	July-August
	Bombus perplexus	10	*Helianthus divaricatus*	July
	Bombus sandersoni	1		

Table 1 (continued).

Family	Species	#	Flower Sweep	Month
Apidae	*Bombus sandersoni/vagans*	2		
	Bombus vagans	13		
	Ceratina calcarata	4	*Hieracium traillii*	June, May
	Ceratina mikmaqi	5	*Fabaceae sp., Asclepias tuberosa*	June
	Ceratina strenua	15	*Eriogonum allenii, Campanula divaricata, H. divaricatus, Hieracium traillii, Penstemon canescens*	May-August
	Eucera atriventris	1		
	Eucera rosae	1		
	Melecta pacifica	4		
	Nomada luteoloides	1	*Viola pedata*	April
	Nomada maculata	2		
	Nomada pygmaea	6	*Packera antennariifolia, Sedum glaucophyllum*	May
	N. seneciophila	1	*Packera antennariifolia*	May
	Panurginus potentillae	1	*Potentilla canadensis*	April
	Pseudopanurgus virginicus	8	*Houstonia sp.*	May-July
	Xylocopa virginica	1	*Asclepias tuberosa*	June
Colletidae	*Hylaeus affinis/modestus*	9	*Penstemon canescens, Sumac compallinum*	May, July

Table 1 (continued)

Family	Species	#	Flower Sweep	Month
Colletidae	*Hylaeus modestus*	7	*Fabaceae sp., Penstemon canescens, Asclepias tuberosa, Sedum glaucophyllum, Euphorbia corollata*	May, July
Halictidae	*Augochlora pura*	375	*Asclepias verticillata, C. divaricata, H. divaricatus, P. antennariifolia, Rhus copallina var. latifolia, Euphorbia corollata, Asclepias tuberosa*	May-August
	Augochlorella aurata	117	*A. verticillata, Boechera serotina, C. divaricata, Erigeron strigosus, Hieracium traillii, P. antennariifolia, P. canadensis, Asclepias tuberosa, E. allenii, H. divaricatus, Euphorbia corollata*	May-August
	Augochloropsis metallica fulgida	1	*Rhus copallina var. latifolia*	July
	Halictus confusus	1	*Helianthus divaricatus*	August
	Halictus ligatus/poeyi	2	*Helianthus divaricatus*	July
	Halictus rubicundus	1		
	Lasioglossum acuminatum	2		
	L. apocyni	1	*Eriogonum allenii*	June
	L.birkmanni	3	*Potentilla canadensis, Sedum glaucophyllum*	May
	L.bruneri	3	*Rhus copallina var. latifolia*	July
	L.coeruleum	1		

Table 1 (continued)

Family	**Species**	**#**	**Flower Sweep**	**Month**
Halictidae	*L. cressonii*	27	*P. antennariifolia, P. canadensis, Asclepias tuberosa, Rhus copallina var. latifolia*	April-July
	L.ephialtum	1	*Sedum glaucophyllum*	May
	L. fattigi	16	*A. cernuum, Rhus copallina var. latifolia, C. divaricata, E. allenii, Hieracium traillii, P. canadensis, Asclepias tuberosa, Sedum glaucophyllum, Houstonia sp.*	May-August
	L.forbesii	1	*Asclepias tuberosa*	June
	L. foxii	8	*Houstonia sp., Packera antennariifolia*	April, June
	L.fuscipenne	1		
	L. gotham	4	*Houstonia sp., Asclepias tuberosa, Euphorbia corollata*	June
	L.hitchensi	1		
	*L.leucozonium**	1		
	L. oblongum	1		
	L. quebecense	1		
	L.smilacinae	1		
	Lasioglossum Sp1	23	*A. cernuum, Hieracium traillii, Houstonia sp., P. canadensis, Asclepias tuberosa, Sedum glaucophyllum*	May-July

Table 1 (continued)

Family	**Species**	**#**	**Flower Sweep**	**Month**
Halictidae	*Lasioglossum Sp2*	2	*Houstonia sp., Potentilla canadensis*	May
	Lasioglossum species	19	*A. verticillata, Hieracium traillii, Houstonia sp., Asclepias tuberosa, Sedum glaucophyllum*	May-June
	L. sub. viridatum	22	*A. verticillata, Houstonia sp., Asclepias tuberosa*	June, July
	L. tegulare	12	*Hieracium traillii, Houstonia sp., Potentilla canadensis, Asclepias verticillata*	May-June
	L. timothyi	8	*Packera antennariifolia, Potentilla canadensis*	April
	L. trigeminum	1		
	L. versatum	29	*Asclepias verticillata, Allium cernuum, Euphorbia corollata*	June, July
Megachilidae	*Anthidiellum notatum*	4	*Fabaceae sp.*	June-August
	Coelioxys sayi	2	*Helianthus divaricatus*	July-August
	Megachile campanulae	9	*A. verticillata, Desmodium paniculatum, Fabaceae sp., Asclepias tuberosa*	June, August
	M. gemula	1	*Asclepias tuberosa*	June
	M. inimica	1	*Helianthus divaricatus*	July
	M. mendica	20	*Boechera serotina, Fabaceae sp., E. allenii, H. divaricatus, Houstonia sp., Asclepias tuberosa, Rhus copallina var. latifolia*	June-August
	Osmia atriventris	1		

Table 1 (continued)

Family	Species	#	Flower Sweep	Month
Megachilidae	*Osmia felti*	2		
	Osmia georgica	1	*Packera antennariifolia*	May
	Osmia pumila	1	*Trifolium virginicum*	May
	*Osmia taurus**	4		

Table 2. Bray-curtis dissimilarity matrix. A higher number between months indicates less similarity between species composition.

	April	**August**	**July**	**June**
August	0.9541985			
July	0.8321678	0.4838710		
June	0.9509202	0.7940379	0.6850394	
May	0.6898396	0.7913043	0.6115702	0.7270588