

WESTERN COLORADO UNIVERSITY

The Thesis Committee for the Graduate Program in MS in Ecology

Certifies that this is the approved version of the following thesis:

**Evaluating differences in bee visitation in small, urban gardens and nearby  
natural areas in West Virginia**

by

Hunter Taylor Benkoski

**APPROVED BY**

---

Robin Bingham, Thesis Advisor

---

Jonathan Coop, Program Director

---

Melanie Armstrong, Dean, School of Environment  
And Sustainability

**18 May 2022**

Date

**Evaluating differences in bee visitation in small, urban gardens and nearby  
natural areas in West Virginia**

by

**Hunter Taylor Benkoski, B.A.**

Thesis

Presented to the Faculty of MS in Ecology

Western Colorado University

in Partial Fulfillment of the for the Degree of

**Master of Science**

Western Colorado University

Gunnison, Colorado

Spring 2022

## **Abstract**

Bee species richness has declined globally in recent decades due to several intertwined factors. Urbanization has both positive and negative effects on bees, with species responses being highly trait- and scale-specific. Urban environments differ from natural environments in the types of habitat and food resources they provide, but they still have the potential to provide valuable habitat to increase bee abundance and diversity. Although research on bee diversity has been conducted in cities, there has been little conducted in small towns, despite their habitat and conservation potential due to their proximity to natural areas and lack of highly developed impervious surface areas. The objective of this study was to evaluate differences in bee floral visitation in backyard gardens and nearby natural areas. In a small town, I surveyed eight sites weekly using a variable transect walk method to capture and identify bees and the flowers they landed on. There were significantly more bees and flowers at the garden sites, and floral abundance was the strongest indicator of bee visitation. The gardens also had slightly later peaks in bee visitation than the natural areas, and there were differences in floral visitation preferences for bees at the two site types. This work will help inform research and conservation practices about the potential of small towns as bee conservation areas.

## Introduction

Bee species richness has declined worldwide (Zattara and Aizen 2021). The decline in abundance and range size of North American bumble bees has been well-documented across numerous species (Gixti et al. 2009, Cameron et al. 2011, Colla et al. 2012, Bushmann and Drummond 2015, Jacobson et al. 2018, Wood et al. 2019), yet potential declines in wild non-*Bombus* species and potential shifts in bee communities are only beginning to be understood (Koh et al. 2016). The intertwined factors that lead to bee declines include changes in land use (Kearns and Inouye 1997, Colla and Packer 2008), pesticide use (Mallinger et al. 2015), introduced parasites and disease (Goulson et al. 2008, Graystock et al. 2014, Cameron et al. 2016), and the effects of climate change (Sirois-Delisle and Kerr 2018).

Several studies have found that bumble bee diversity decreases with increasing levels of urbanization (Ahrné et al. 2009, Fortel et al. 2014). Urban environments are highly heterogeneous, however, and have also been described as havens for bees where diversity, abundance (Hall et al. 2017), and reproductive success (Samuelson et al. 2018) can be greater than in surrounding landscapes. Wenzel et al. (2020) found that bee responses to urbanization were highly trait- and scale-specific, with cavity nesters and generalist foragers usually responding better than ground nesters and specialized foragers.

Urban environments are often characterized by the amount of impervious surface present (Liu et al. 2014), with greater abundances of impervious surfaces near city centers and industrial areas. The terms “urban”, “semi-urban”, and “rural” are not universally defined within bee research literature, and many studies do not differentiate between different types of rural sites (Verboven et al. 2014). Furthermore, most urban pollinator studies are conducted in large cities

(Wenzel et al. 2020) with less research conducted in smaller towns. Despite the lack of research, small towns are potentially valuable areas for bee research and conservation due to their similarity to more well-studied areas of urban sprawl where proximity to natural and seminatural habitats (Steffan-Dewenter 2002), lower levels of impervious surfaces compared to more highly urbanized areas (Fortel et al. 2014), and large proportions of suitable foraging and nesting resources (Majewska et al. 2018) have been connected to positive pollinator biodiversity outcomes (Wenzel et al. 2020).

There is a need for studies evaluating bee communities in small towns to better understand and inform management decisions unique to the characteristics and needs of those areas. The objective of this study, therefore, is to answer the following questions:

- 1) Does the abundance of foraging bees vary between backyard gardens in small towns and nearby natural areas?
- 2) Is floral abundance a stronger indicator of bee floral visitation than site type, surrounding area, or floral species composition?
- 3) Does bee floral visitation vary temporally between backyard gardens in small towns and nearby natural areas?
- 4) Do the plant-pollinator relationships vary between backyard gardens in small towns and nearby natural areas?

## Methods

### Study system and site selection

The study was conducted from March 30<sup>th</sup> – September 4<sup>th</sup>, 2021 in Williamstown, West Virginia. Williamstown is in Wood County along the Ohio River. It is about 4.69 square kilometers in size with a population of just under 3,000 people. It has a humid continental climate with mean annual temperatures of about 13 degrees Celsius. The average low in January is -5°C and the average high in July is 29.4°C with an average of 18 days annually with highs above 32.2°C. July is the most humid month, and the area gets an average of 106 centimeters of rain per year (“Weather averages Williamstown, West Virginia” n.d.).

In the study region, I selected eight sampling sites – four in backyard gardens in town and four in nearby natural areas (Figure 1).

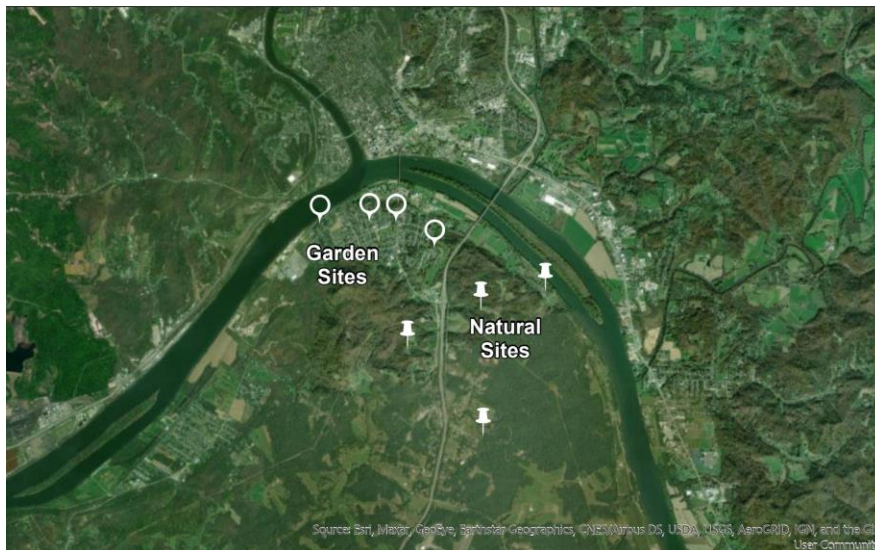


Figure 1. Location of eight study sites – four gardens (Tomlinson Mansion, Armstrong Garden, Molly’s Garden, and Lori’s Garden) and four natural areas (Suzannah’s Field, Robert’s Field, Jason’s Field, and Ohio River Islands National Wildlife Refuge (ORINWR) Field) – in Williamstown, West Virginia. All the natural sites were at least one kilometer away from the garden sites.

The natural area sites were all located at least 1km away from the backyard gardens to maintain sample independence (Osborne et al. 1999, Cresswell et al. 2000, Hagen et al. 2011). I selected a 100m<sup>2</sup> area for each natural site. I chose an area of 100m<sup>2</sup> because my smallest garden site was about that size. I divided each natural area (all of which were fields) into 100m<sup>2</sup> sections and numbered the sections then used a random number generator to select which section would be my sample plot. Although the potential foraging habitat for bees was greater than 100m<sup>2</sup> for most of my sites, I only sampled within the designated sample plots so the measurements of bee abundance and floral abundance would be comparable among the sites and site types.

#### Plot-level variables

Each site was composed of ten, 10m<sup>2</sup> subplots which I used for floral abundance estimates. In each subplot, I identified all flowering plant species and then quantified floral abundance by estimating the percentage of each subplot that was covered by flowering plants. Temperature and wind speed were recorded using a Kestrel 3000 Handheld Weather Meter. I also noted the cloud cover (clear, partly cloudy, or mostly cloudy) and made general weather observations. These estimates were recorded at the beginning of each survey.

#### Bee surveys

I surveyed each site approximately once every seven days during peak insect activity when temperatures were at least 10°C and skies were clear or partly cloudy (LeBuhn et al. 2003). For each sampling period, I recorded my survey start time and conducted either 15 or 30 minutes of bee hand netting (the sampling time does not include the time spent handling, marking, identifying, or releasing bees) using a variable transect walk method (Westphal et al. 2008). The variable transect walk method is particularly well-suited for backyard gardens where attractive

floral resources are set in patches within lawns that are unlikely to be attractive to foraging bees. It is well documented that hand netting biases the sampler to catch larger bees that are more visible compared to other bee sampling methods (such as pan traps) that bias toward smaller bees (Krahner et al. 2021). Hand netting is also more likely to capture more species overall than pan traps (Manyuli 2012). The choice to do hand netting and avoid other sampling methods was primarily logistically driven: to avoid identification and pinning “bottlenecking” (Woodard et al. 2020) and to avoid the destructive sampling of bees. I caught any bee that I saw land on an open flower. Once captured, I kept small bees in vials in a cooler until the end of the survey to prevent re-capture during the sampling period. I marked larger bees, such as bumble bees and carpenter bees, with a dot of paint on the thorax and released them. Each site had its own paint pen color to ensure sites were independent, and I did not re-capture bees that already had a dot of paint (I never saw a marked bee with a paint color that did not correspond to the site I was visiting).

### Bee identification

I classified the captured bees into one of six functional groups: small black solitary bees (sbsb), shiny green bees (green), large black solitary bees (lbsb), honeybees (*Apis mellifera*), bumble bees (*Bombus spp.* identified to species level), or carpenter bees (*Xylocopa virginica*). These classifications were based on non-microscopic identification characteristics and life history traits. I recommend that other researchers working with functional group designations set clear definitions for what measurable characteristics they use to fit bees into these categories (e.g., bee length, the presence of pollen on the underside of the abdomen, etc.). Despite the reduced specificity with the way I designated sbsb and lbsb, the two groups appeared to have distinct foraging preferences, especially in the natural sites. This suggests that the designations maintained enough accuracy to delineate different preferences because of the distinct life history



traits of the two functional groups. I lethally sampled a few bees (less than ten out of over 2,500) to confirm identification using microscopic characteristics.

### Statistical analysis

I conducted all statistical analyses using R Statistical Software version 4.1.2 (R Core Team 2021). To answer questions 1 and 2, I ran generalized linear models (GLMs) with bee abundance as the response variable in response to site type, floral abundance, floral species richness, and floral abundance & floral species richness with Poisson distributions (function `glm`, package “stats”). I used the `tab_model` function (package “sjPlot”) to analyze the statistical significance of these relationships and the `ggplot` function (package “ggplot2”) to visualize these relationships with boxplots and scatterplots. To answer question 3, I created an area under the curve plot that visualizes bee abundance over time at the two site types (function `ggplot`, package “ggplot2”). This plot utilizes the functions `geom_smooth` and `stat_smooth` functions. To answer question 4, I created network plots to visualize the plant-pollinator interactions at the two site types (function `plotweb`, package “bipartite”).

## **Results**

I visited the sites 126 times (14 – 17 visits per site and 63 visits per site type) between March 30<sup>th</sup> and September 4<sup>th</sup> of 2021. I caught 2,504 bees - 933 bumble bees, 618 small black solitary bees, 600 honeybees, 187 green bees, 110 carpenter bees, 54 large black solitary bees, and 2 unknown bees. Of the bumble bees, there were 507 *B. impatiens*, 260 *B. bimaculatus*, 160 *B. griseocollis*, 2 *B. perplexus*, 2 *B. auricomus*, 1 *B. vagans*, and 1 *B. fervidus* (Table 1).

Bee Group	Early Season	Mid-Season	Late Season
Garden Sites			
Sbsb	66	164	217
Lbsb	2	6	23
Green	3	58	45
<i>X. virginica</i>	8	17	85
<i>A. mellifera</i>	46	61	328
<i>Bombus spp.</i>	4	413	366
<i>B. impatiens</i>	0	75	353
<i>B. bimaculatus</i>	4	223	1
<i>B. griseocollis</i>	0	112	11
<i>B. perplexus</i>	0	1	0
<i>B. auricomus</i>	0	2	0
<i>B. vagans</i>	0	0	0
<i>B. fervidus</i>	0	0	1
Unknown	0	0	0
Natural Sites			
Sbsb	60	70	41
Lbsb	0	16	7
Green	21	42	18
<i>X. virginica</i>	0	0	0
<i>A. mellifera</i>	4	115	46
<i>Bombus spp.</i>	0	120	30
<i>B. impatiens</i>	0	52	27
<i>B. bimaculatus</i>	0	31	1
<i>B. griseocollis</i>	0	36	1
<i>B. perplexus</i>	0	1	0
<i>B. auricomus</i>	0	0	0
<i>B. vagans</i>	0	0	1
<i>B. fervidus</i>	0	0	0
Unknown	0	2	0

Table 1. Bees caught on flowers in garden and natural sites throughout the sampling season (early = March to mid-May; mid = mid-May to mid-July; late = mid-July to end of September). Groups include small black solitary bees (sbsb), large black solitary bees (lbsb), green bees (green), carpenter bees (*X. virginica*), all bumble bees (*Bombus spp.*), common eastern bumblebee (*B. impatiens*), two-spotted bumblebee (*B. bimaculatus*), brown-belted bumblebee (*B. griseocollis*), confusing bumblebee (*B. perplexus*), black and gold bumblebee (*B. auricomus*), half-black bumblebee (*B. vagans*), golden northern bumblebee (*B. fervidus*), and unidentified bees (unknown).

Bees were caught on 107 different flower species in the gardens and 34 different flower species in the natural areas (Table 2).

<b>Plant Family</b>	<b>Plant Species</b>	<b>Site</b>
Acanthaceae	Thunbergia alata	Garden
Amaranthaceae	Celosia argentea	Garden
Amaranthaceae	Celosia sp.	Garden
Amaryllidaceae	Allium senescens	Garden
Apiaceae	Daucus carota	Garden & Natural
Apiaceae	Eryngium sp.	Garden
Apiaceae	Foeniculum vulgare	Garden
Apocynaceae	Apocynum cannabinum	Natural
Apocynaceae	Asclepias incarnata	Garden
Apocynaceae	Asclepias purpurascens	Garden
Apocynaceae	Asclepias sp.	Garden
Apocynaceae	Asclepias syriaca	Natural
Apocynaceae	Asclepias tuberosa	Garden & Natural
Araceae	Zantedeschia sp.	Garden
Asparagaceae	Hosta sp.	Garden
Asphodelaceae	Hemerocallis liliosphodelus	Garden
Asteraceae	Achillea millefolium	Natural
Asteraceae	Achillea sp.	Garden
Asteraceae	Bellis perennis	Garden
Asteraceae	Centaurea cyanus	Garden
Asteraceae	Chrysanthemum leucanthemum	Natural
Asteraceae	Cirsium discolor	Natural
Asteraceae	Coreopsis sp.	Garden
Asteraceae	Dahlia pinnata	Garden
Asteraceae	Echinacea paradoxa	Garden
Asteraceae	Echinacea purpurea	Garden
Asteraceae	Echinacea sp.	Garden
Asteraceae	Erigeron philadelphicus	Garden & Natural
Asteraceae	Erigeron sp.	Natural
Asteraceae	Eupatorium coelestinum	Natural
Asteraceae	Eutrochium purpureum	Garden
Asteraceae	Eupatorium sp.	Garden
Asteraceae	Gaillardia pulchella	Garden
Asteraceae	Helianthus annuus	Garden
Asteraceae	Helianthus sp.	Garden
Asteraceae	Heliopsis helianthoides	Garden
Asteraceae	Ligularia dentata	Garden
Asteraceae	Rudbeckia hirta	Garden
Asteraceae	Sanvitalia procumbens	Garden
Asteraceae	Solidago juncea	Natural
Asteraceae	Solidago sp.	Garden
Asteraceae	Taraxacum officinale	Garden & Natural

Asteraceae	<i>Tithonia rotundifolia</i>	Garden
Asteraceae	<i>Zinnia</i> sp.	Garden
Balsaminaceae	<i>Impatiens balsamina</i>	Garden
Boraginaceae	<i>Borago officinalis</i>	Garden
Boraginaceae	<i>Cynoglossum</i> sp.	Garden
Brassicaceae	<i>Allaria petiolata</i>	Garden
Brassicaceae	<i>Cardamine hirsuta</i>	Garden
Brassicaceae	<i>Cardamine</i> sp.	Garden
Brassicaceae	<i>Erysimum cheiri</i>	Garden
Brassicaceae	<i>Lobularia maritima</i>	Garden
Brassicaceae	<i>Rorippa sylvestris</i>	Garden
Campanulaceae	<i>Lobelia inflata</i>	Garden
Campanulaceae	<i>Platycodon</i> sp.	Garden
Caprifoliaceae	<i>Lonicera maackii</i>	Garden
Caprifoliaceae	<i>Scabiosa columbaria</i>	Garden
Caryophyllaceae	<i>Cerastium tomentosum</i>	Garden
Caryophyllaceae	<i>Stellaria media</i>	Garden
Commelinaceae	<i>Tradescantia</i> sp.	Garden
Commelinaceae	<i>Tradescantia virginica</i>	Garden
Cornaceae	<i>Cornus sericea</i>	Garden
Crassulaceae	<i>Sedum</i> sp.	Garden
Dipsacaceae	<i>Knautia arvensis</i>	Garden
Eleagnaceae	<i>Elaeagnus umbellata</i>	Natural
Fabaceae	<i>Baptisia</i> sp.	Garden
Fabaceae	<i>Cercis canadensis</i>	Garden
Fabaceae	<i>Desmodium</i> sp.	Natural
Fabaceae	<i>Lupinus</i> sp.	Garden
Fabaceae	<i>Trifolium agrarium</i>	Natural
Fabaceae	<i>Trifolium pratense</i>	Natural
Fabaceae	<i>Trifolium repens</i>	Garden & Natural
Geraniaceae	<i>Geranium carolinianum</i>	Garden
Hydrangeaceae	<i>Hydrangea paniculata</i>	Garden
Hydrangeaceae	<i>Hydrangea</i> sp.	Garden
Hypericaceae	<i>Hypericum perforatum</i>	Natural
Lamiaceae	<i>Agastache foeniculum</i>	Garden
Lamiaceae	<i>Glechoma hederacea</i>	Garden & Natural
Lamiaceae	<i>Lamium purpureum</i>	Garden
Lamiaceae	<i>Lavandula</i> sp.	Garden
Lamiaceae	<i>Mentha arvensis</i>	Natural
Lamiaceae	<i>Monarda</i> sp.	Garden
Lamiaceae	<i>Nepeta cataria</i>	Garden
Lamiaceae	<i>Origanum vulgare</i>	Garden
Lamiaceae	<i>Prunella vulgaris</i>	Natural

Lamiaceae	<i>Pycnanthemum incanum</i>	Garden
Lamiaceae	<i>Pycnanthemum tenuifolium</i>	Garden & Natural
Lamiaceae	<i>Salvia guaranitica</i>	Garden
Lamiaceae	<i>Salvia nemorosa</i>	Garden
Lamiaceae	<i>Salvia</i> sp.	Garden
Lamiaceae	<i>Salvia yangii</i>	Garden
Lamiaceae	<i>Stachys officinale</i>	Garden
Lamiaceae	<i>Thymus citriodorus</i>	Garden
Liliaceae	<i>Tulipa gesneriana</i>	Garden
Liliaceae	<i>Tulipa hungarica</i>	Garden
Lythraceae	<i>Cuphea hyssopifolia</i>	Garden
Lythraceae	<i>Cuphea</i> sp.	Garden
Montiaceae	<i>Claytonia virginica</i>	Natural
Oenotheraceae	<i>Oenothera</i> sp.	Garden
Oleaceae	<i>Forsythia</i> sp.	Garden
Onagraceae	<i>Oenothera perennis</i>	Natural
Oxalidaceae	<i>Oxalis europaea</i>	Garden
Oxalidaceae	<i>Oxalis</i> sp.	Garden & Natural
Papaveraceae	<i>Papaver californicum</i>	Garden
Persicariaceae	<i>Persicaria</i> sp.	Garden
Plantaginaceae	<i>Penstemon digitalis</i>	Natural
Plantaginaceae	<i>Penstemon</i> sp.	Garden
Plantaginaceae	<i>Veronica persica</i>	Garden
Plantaginaceae	<i>Veronica serpyllifolia</i>	Garden
Polygalaceae	<i>Polygala sanguinea</i>	Natural
Ranunculaceae	<i>Anemone coronaria</i>	Garden
Ranunculaceae	<i>Aquilegia vulgaris</i>	Garden
Ranunculaceae	<i>Delphinium</i> sp.	Garden
Ranunculaceae	<i>Helleborus orientalis</i>	Garden
Rosaceae	<i>Agrimonia parviflora</i>	Natural
Rosaceae	<i>Duchesnea indica</i>	Garden
Rosaceae	<i>Geum chilloense</i>	Garden
Rosaceae	<i>Potentilla simplex</i>	Garden & Natural
Rosaceae	<i>Rosa multiflora</i>	Natural
Rosaceae	<i>Rosa palustris</i>	Natural
Rosaceae	<i>Rubus allegheniensis</i>	Natural
Rosaceae	<i>Rubus</i> sp.	Garden
Rubiaceae	<i>Houstonia caerulea</i>	Natural
Saxifragaceae	<i>Astilbe</i> sp.	Garden
Saxifragaceae	<i>Heuchera</i> sp.	Garden
Saxifragaceae	<i>Heuchera villosa</i>	Garden
Scrophulariaceae	<i>Buddleja davidii</i>	Garden
Solanaceae	<i>Calibrachoa</i> sp.	Garden

Verbenaceae	Lantana camara	Garden
Verbenaceae	Verbena bonariensis	Garden
Vernoniaceae	Vernonia sp.	Natural
Violaceae	Viola sp.	Garden

Table 2. Flowering plant species that were visited by bees at garden and natural sites.

Does the abundance of foraging bees vary between backyard gardens in small towns and nearby natural areas?

There were significantly more bees caught at the garden sites than at the natural sites, with 1,912 bees at the garden sites and 592 bees at the natural sites ( $p < 0.001$ ; Figure 2).

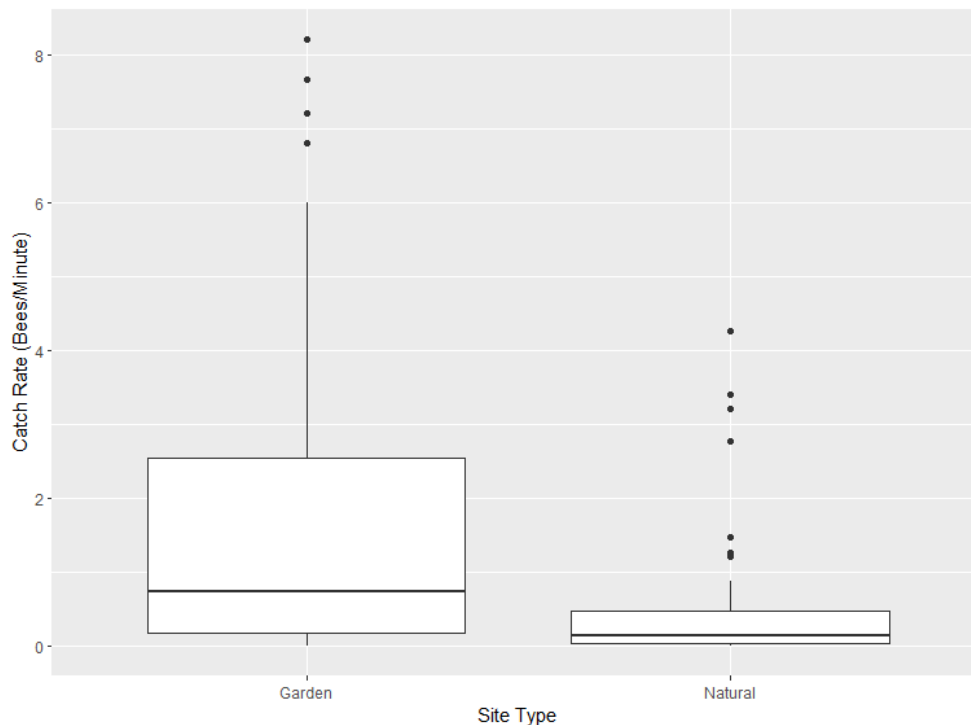


Figure 2. The catch rate of bees (measured as bees captured per minute) in response to site type (garden and natural). There was a significantly higher catch rate of bees in garden sites than in natural sites ( $p < 0.001$ ).

There were significantly more small black solitary bees ( $p < 0.001$ ), *A. mellifera* ( $p = 0.003$ ), *B. bimaculatus* ( $p = 0.029$ ), and *B. impatiens* ( $p < 0.001$ ) at the garden sites. There was no

significant difference in abundance at the site types for large black solitary bees ( $p = 0.579$ ), *X. virginica* ( $p = 0.995$ ), green bees ( $p = 0.444$ ), and *B. griseocollis* ( $p = 0.122$ ; Table 3).

Model Term	Coef	SE	Z	p
Intercept	0.597	0.093	6.393	<0.001
Overall catch rate	-1.370	0.208	-6.499	<0.001
Intercept	-0.891	0.197	-4.531	<0.001
Sbsb catch rate	-1.190	0.407	-2.920	0.0035
Intercept	-3.417	0.696	-4.913	<0.001
Lbsb catch rate	-0.661	1.192	-0.555	0.579
Intercept	-2.324	0.403	-5.771	<0.001
Green catch rate	-0.502	0.6557	-0.765	0.444
Intercept	-2.152	0.370	-5.824	<0.001
<i>X. virginica</i> catch rate	-19.150	3228.346	-0.006	0.995
Intercept	-0.833	0.191	-4.361	<0.001
<i>A. mellifera</i> catch rate	-1.135	0.388	-2.929	0.003
Intercept	-0.785	0.187	-4.209	<0.001
<i>B. impatiens</i> catch rate	-1.861	0.509	-3.659	<0.001
Intercept	-1.851	0.318	-5.823	<0.001
<i>B. bimaculatus</i> catch rate	-2.197	1.005	-2.186	0.0288
Intercept	-2.271	0.392	-5.791	<0.001
<i>B. griseocollis</i> catch rate	-1.322	0.855	-1.546	0.122

Table 3. Results from models evaluating the relationship between site type (independent variable) and bee catch rates (dependent variables). Presented are the coefficients (Coef), standard error of coefficient estimates (SE), Z scores (Z), and p-values (p).

*Is floral abundance a stronger indicator of bee floral visitation than site type, surrounding area, or floral species composition?*

There was significantly higher floral abundance at the garden sites than at the natural sites ( $p < 0.001$ ; Figure 3).

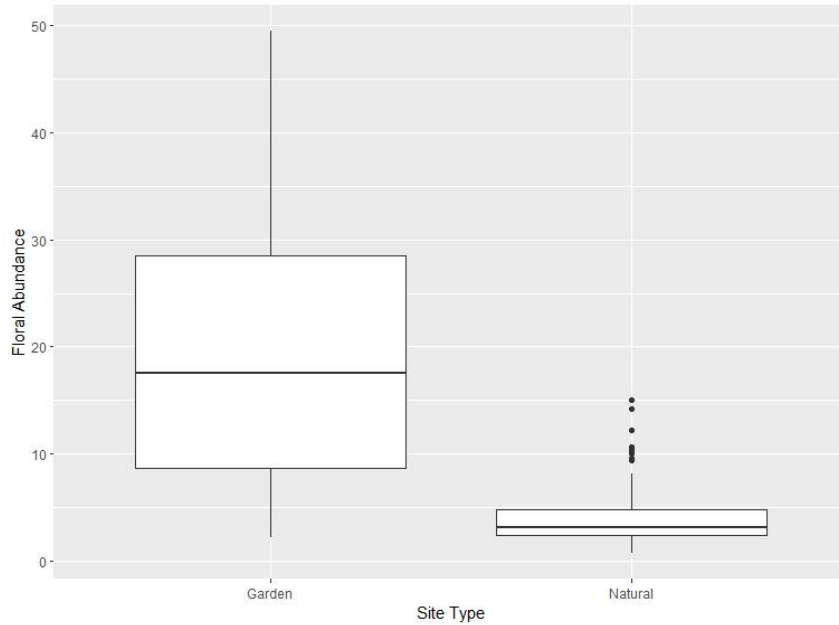


Figure 3. The abundance of flowers (measured as percentage of site covered in flowering plants) in response to site type (garden and natural). There was a significantly lower abundance of flowers in natural sites than in garden sites ( $p < 0.001$ ).

Floral abundance was a stronger indicator of bee abundance ( $p < 0.001$ ) than floral species richness ( $p = 0.034$ ), site type ( $p = 0.192$ ), and floral abundance & floral species richness ( $p = 0.010$ ; Table 4).

<b>Model Term</b>	<b>Coef</b>	<b>SE</b>	<b>Z</b>	<b>p</b>
Intercept	-1.998	0.496	-4.026	<0.001
Floral abundance	0.103	0.016	6.426	<0.001
Floral species richness	0.039	0.018	2.115	0.034
Site type	0.489	0.375	1.305	0.192
Floral abundance & floral species richness	-0.001	0.001	-2.582	0.010

Table 4. Results from models evaluating the relationship between floral abundance, floral species richness, site type, and floral abundance x floral species richness (independent variables) and bee catch rates (dependent variable). Presented are the coefficients (Coef), standard error of coefficient estimates (SE), Z scores (Z), and p-values (p).

*Does bee floral visitation vary temporally between backyard gardens in small towns and nearby natural areas?*



Temporally, bee visitation was similar across the two site types with natural area visitation almost entirely overlapping with garden visitation. However, the natural areas saw a small visitation peak in early April and the highest visitation in early July while the gardens had a delayed small visitation peak in early May and the highest visitation in late July (Figure 4).

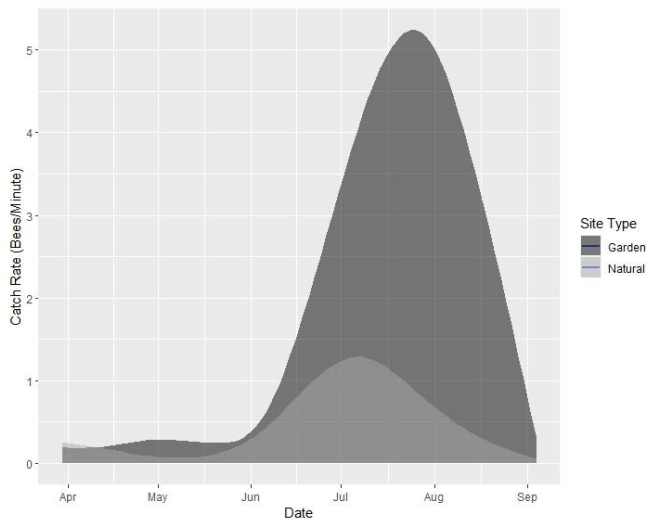


Figure 4. The catch rate of bees (measured as bees captured per minute) over time at two site types (garden and natural).

Peak floral abundance for the gardens was in late July, and the floral abundance at the natural sites was relatively constant through the sampling season (Figure 5). In the natural areas, *Claytonia virginica* bloomed from March 30<sup>th</sup> to May 12<sup>th</sup>, *Pycnanthemum tenuifolium* June 14<sup>th</sup> to August 4<sup>th</sup>, *Apocynum cannabinum* June 15<sup>th</sup> to June 26<sup>th</sup>, *Asclepias syriaca* June 17<sup>th</sup> to July 9<sup>th</sup>, and *Asclepias tuberosa* from June 23<sup>rd</sup> to July 28<sup>th</sup>. In the gardens, *Forsythia sp.* bloomed from March 30<sup>th</sup> to April 13<sup>th</sup>, *Glechoma hederacea* April 3<sup>rd</sup> to May 21<sup>st</sup>, *Hosta sp.* June 14<sup>th</sup> to August 29<sup>th</sup>, *Asclepias incarnata* June 15<sup>th</sup> to July 7<sup>th</sup>, *Verbena bonariensis* June 15<sup>th</sup> to August 5<sup>th</sup>, *Echinacea purpurea* June 15<sup>th</sup> to August 25<sup>th</sup>, *Eryngium sp.* June 15<sup>th</sup> to July 7<sup>th</sup>, *Buddleja davidii* June 22<sup>nd</sup> to September 4<sup>th</sup>, *Rudbeckia hirta* July 2<sup>nd</sup> to August 29<sup>th</sup>, and *Pycnanthemum incanum* from July 7<sup>th</sup> to September 2<sup>nd</sup>.

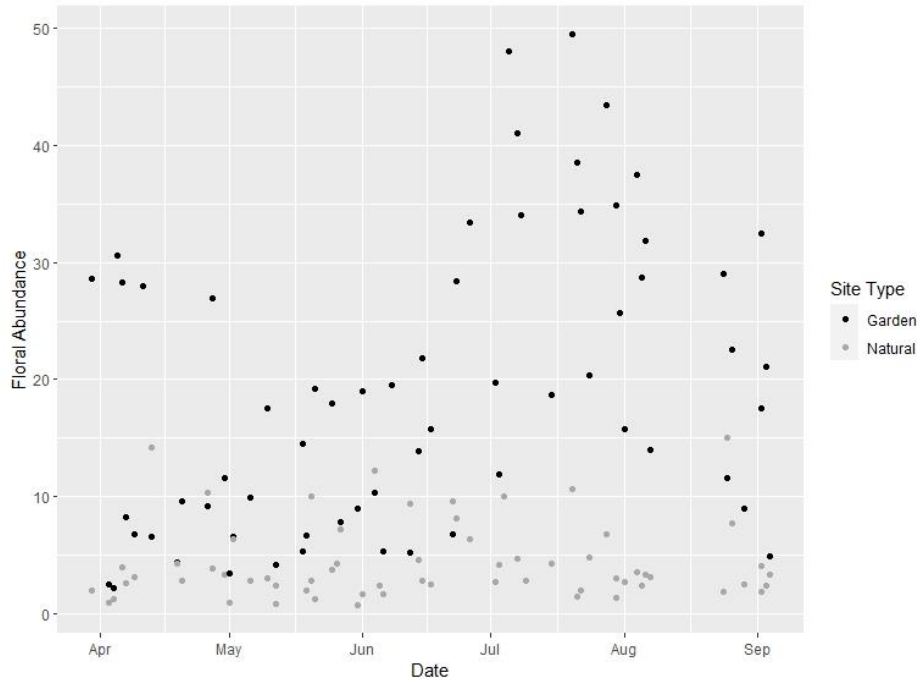


Figure 5. The abundance of flowers (measured as percentage of site area covered in flowering plants) over time at each site type (garden or natural). Peak floral abundance was in late July for the gardens. Floral abundance was relatively constant across the sampling period for the natural sites.

*Do the plant-pollinator relationships vary between backyard gardens in small towns and nearby natural areas?*

At the natural sites, small black solitary bees visited the greatest diversity of flowers and were caught mostly on Virginia spring beauty (*Claytonia virginica*). Several flowers were only visited by small black solitary bees, including Quaker ladies (*Houstonia caerulea*), wood sorrel (*Oxalis sp.*), early goldenrod (*Solidago juncea*), white clover (*Trifolium repens*), daisy (*Erigeron sp.*), and small sundrops (*Oenothera perennis*). The green bees overlapped in the diversity of their floral visitation preferences with the small black solitary bees, but the green bees notably also visited butterflyweed (*Asclepias tuberosa*) more heavily than the small black solitary bees. The large black solitary bees visited a smaller diversity of flowers than the small black solitary bees, and there were several flowers that they visited that were not among the small black

solitary bees' visitation, including tick clover (*Desmodium sp.*) and purple milkwort (*Polygala sanguinea*). The large black solitary bees also visited the foxglove beardtongue (*Penstemon digitalis*) more than the small black solitary bees. *A. mellifera* was very prevalent on narrowleaf mountain mint (*Pycnanthemum tenuifolium*) and *Asclepias tuberosa*. Each of the three prominent *Bombus* species showed distinct floral preferences. *B. bimaculatus* primarily visited *Asclepias tuberosa*, *B. impatiens* primarily visited *Pycnanthemum tenuifolium*, and *B. griseocollis* primarily visited common milkweed (*Asclepias syriaca*). *B. impatiens* showed a bit more diversity in its foraging patterns than the other two bee species in the natural areas (Figure 6).

At the garden sites, all the bee functional groups visited a greater diversity of flowers than the bees at the natural areas. Like the natural sites, small black solitary bees visited the greatest diversity of plants and were the only bee group to visit numerous flower species, including garlic mustard (*Allaria petiolate*), poppy anemone (*Anemone coronaria*), common columbine (*Aquilegia vulgaris*), common daisy (*Bellis perennis*), hairy bittercress (*Cardamine hirsute*), toothwort (*Cardamine sp.*), snow-in-summer (*Cerastium tomentosum*), eastern redbud (*Cercis canadensis*), dahlia (*Dahlia pinnata*), Queen Anne's lace (*Daucus carota*), delphinium (*Delphinium sp.*), mock strawberry (*Duchesnea indica*), forsythia (*Forsythia sp.*), Carolina geranium (*Geranium carolinianum*), Chilean avens (*Geum chiloense*), yellow day lily (*Hemerocallis lilioasphodelus*), hydrangea (*Hydrangea sp.*), sweet alyssum (*Lobularia maritima*), tall wood sorrel (*Oxalis europaea*), wood sorrel (*Oxalis sp.*), blue balloon flower (*Platycodon sp.*), common cinquefoil (*Potentilla simplex*), narrowleaf mountain min (*Pycnanthemum tenuifolium*), creeping yellow-cress (*Rorippa sylvestris*), blackberry (*Rubus sp.*), goldenrod (*Solidago sp.*), chickweed (*Stellaria media*), thyme-leaved speedwell (*Veronica serpyllifolia*), creeping zinnia (*Sanvitalia procumbens*), garden tulip (*Tulipa gesneriana*), and

violet (*Viola sp.*). *B. griseocollis* primarily visited swamp milkweed (*Asclepias incarnata*), notably in the same genus as its preferred natural area flower. *B. impatiens* visited a wide range of flowers in the gardens, and *B. bimaculatus* likewise showed a much greater diversity of floral visitation in the gardens than it showed in the natural areas. *X. virginica* were only present in the garden sites, and they were mostly caught on butterflybush (*Buddleja davidii*) (Figure 7).

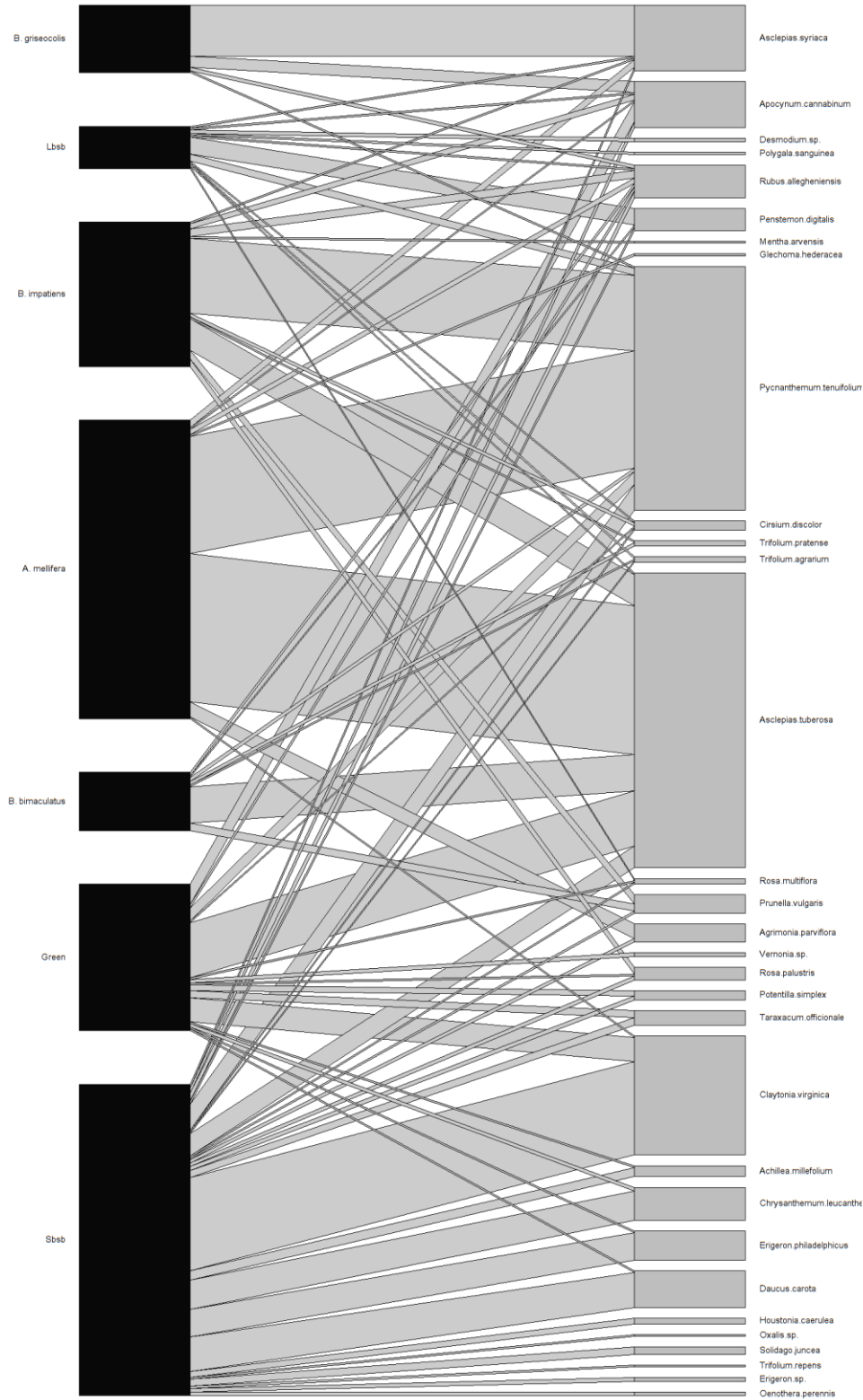


Figure 6. Plant-pollinator relationships at Natural sites. Bee functional groups are on the left and flower species on the right. The thickness of the boxes represents the quantity of bees/flowers, and the thickness of the lines connecting them represents the number of times a bee from that group was caught on a flower species.

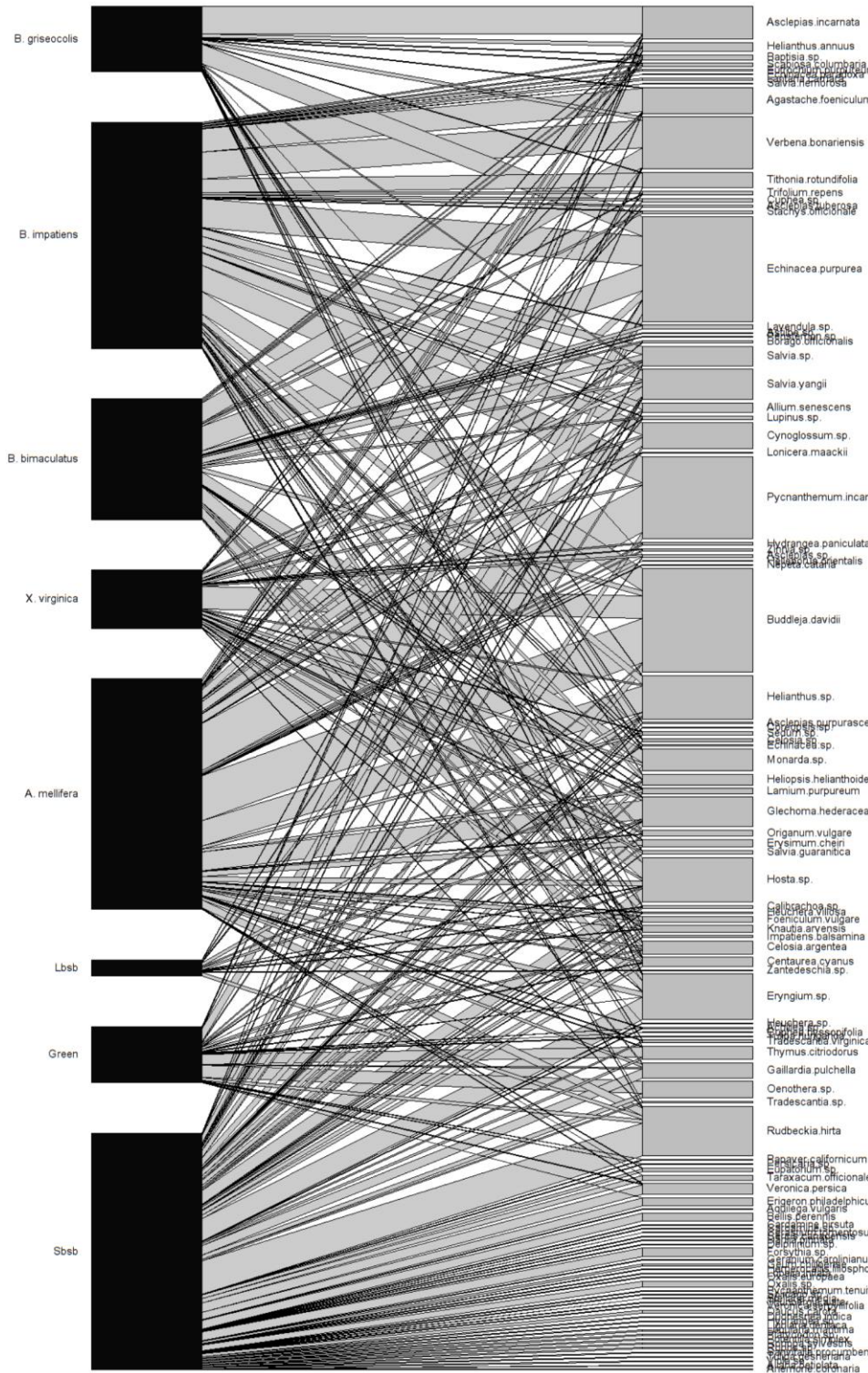


Figure 7. Plant-pollinator relationships at Garden sites. Bee functional groups are on the left and flower species on the right. The thickness of the boxes represents the quantity of bees/flowers, and the thickness of the lines connecting them represents the number of times a bee from that group was caught on a flower species.

## Discussion

Urban environments may provide different types of floral resources than natural environments, but they have the potential to support bee populations through their unique floral composition and abundance. I found that there were significantly more bees in the garden sites than in the natural area sites. Floral abundance, which was higher in the gardens, was a stronger indicator of bee abundance than floral species richness, site type, and floral species richness & site type combined. The gardens also had greater floral species richness and later bee abundance peaks than the natural areas, with bees visiting a greater diversity of flowers at those garden sites.

While I found that the gardens had significantly more bees than the nearby natural areas, research is mixed as to which habitat type is better for bee abundance. Some studies have found that gardens support greater bee abundance and/or biodiversity than surrounding natural areas (Lowenstein et al. 2014; Hal et al. 2016), while others have found the opposite (Bates et al. 2014; Lagucki et al. 2017). Likewise, gardens have shown greater bee abundance than nearby agricultural land that is low in floral resource availability (Martins et al. 2017). My finding that floral abundance was the strongest predictor of bee abundance aligns with the literature that floral abundance is the key driver of bee abundance (Gerner and Sargent 2022). This suggests that natural areas and gardens both have the potential to support bee abundance if they have appropriate floral resources available.

However, not all flowers are created equally when it comes to providing food. For example, perennial plants tend to provide higher quality pollen and nectar than annuals, and plants with numerous flowers instead of one big showy flower tend to be more preferred by bees. Bees, like flowers, are diverse and exhibit unique foraging preferences depending on their size,

tongue length, active period, and so much more! A general management rule of thumb for gardeners is to plant diverse, native flowers that have the potential to attract a diversity of bees. This means including flowers with different shapes, sizes, bloom times, and colors in gardens. Native flowers are often attractive to bees because they co-evolved together, and, as a bonus, they are often lower maintenance than their non-native counterparts since they are adapted to the region's climate.

*Claytonia virginica* was among the first flowers to bloom in early April, and it was almost entirely only present in the natural areas. Small black solitary bees and green bees were the primary visitors to this species. At the garden sites, there were few flowers planted at this time. The species that were planted at this time, primarily tulips and daffodils, were not often visited by bees. The early-season flowers that ended up being most visited by the first wave of pollinators in the gardens were the “weeds” that became more abundant in mid-April to early May. These included *Glechoma hederacea*, *Taraxacum officinale*, and *Veronica persica*. These weeds played a counter-intuitively important role as a food source for early-season bees in the gardens that otherwise had little food available.

Several other studies have found that “weeds” (non-desirable and typically non-native plants) can provide important foraging opportunities for bees in urban landscapes (Larson and Kesheimer 2014; Lowenstein et al. 2018). This begs the question of whether “weeds” are appropriate to allow in gardens. Some species, such as dandelions and Persian speedwell may be suitable garden bed dwellers since they are not considered invasive (in the state of West Virginia). However, *Glechoma hederacea*, is listed as an invasive species (due to the dense patches it forms that can shade out native plants and because it is toxic to many vertebrates) and should be removed and maintained as such. At the moment, “weeds” are filling the ecological



niche in the gardens I visited that *Claytonia virginica* and other native spring ephemeral flowers otherwise fill in natural areas. I recommend that homeowners actively cultivate *Claytonia virginica* and other native spring ephemerals to provide quality early-season foraging opportunities for bees. Generally, gardeners should aim to have plants that bloom through the entire growing season from beginning to end. I also recommend that they be a touch less vigorous about killing off every non-invasive “weed” in the early spring, especially if that means they use fewer pesticides in the process.

The only notable early season planted flower in the gardens that received pollinator visitation was *Forsythia*. This was well-visited by small black solitary bees and green bees alike, but there was not much *Forsythia* planted in my garden sites. The gardens likely had their peak bee abundance later in the summer because there was greater floral abundance in the gardens than in the natural areas at this time. Late July was drier than earlier in the spring/summer, and the natural areas had floral abundance generally decline as the drier weather set in. The gardens, on the other hand, were watered by homeowners and were less constrained by reduced water availability. This was reflected in the time frame in which the more highly visited flower species were present at the two site types. In the natural areas, *Claytonia virginica* bloomed between March 30<sup>th</sup> and May 12<sup>th</sup>. The other highly visited plant species (*Pycnanthemum tenuifolium*, *Apocynum cannabinum*, *Asclepias syriaca*, and *Asclepias tuberosa*) primarily bloomed between mid-June and mid-July. In the gardens, *Forsythia sp.* and *Glechoma hederacea* bloomed between early April and late May. The other highly visited plant species (*Hosta sp.*, *Asclepias incarnata*, *Verbena bonariensis*, *Echinacea purpurea*, *Eryngium sp.*, *Buddleja davidii*, *Rudbeckia hirta*, and *Pycnanthemum incanum*) bloomed between mid-June and late August.

The bee community composition was similar between the two site types, with bumble bees being the most abundant, followed by small black solitary bees, *Apis mellifera*, green bees, *Xylocopa virginica* (gardens only), then large black solitary bees. At both site types, small black solitary bees exhibited unique floral preferences and visited several plant species that no other functional group did. Likewise, small black solitary bees visited the greatest diversity of flowers compared to the other bee functional groups. Geslin et al. (2013) found that solitary bees visited a greater diversity of flower species than *Apis mellifera* and *Bombus spp.* across several different types of habitats, ranging from semi-natural to urban. It makes sense that this would be the case since solitary bees are quite diverse in themselves and many solitary bees are wide-ranging generalists.

At both sites, each of the three prominent *Bombus* species – *B. impatiens*, *B. bimaculatus*, and *B. griseocollis* – exhibited unique floral preferences. This was particularly pronounced in the natural sites where *B. impatiens* preferred *Pycnanthemum tenuifolium*, *B. bimaculatus* preferred *Asclepias tuberosa*, and *B. griseocollis* preferred *Asclepias syriaca*. In the gardens, both *B. impatiens* and *B. bimaculatus* showed much more diversity in their floral visitation with no strong apparent preferences for a single plant species. There were also significantly more of these two species present in the gardens than in the natural areas. *B. griseocollis*, however, mostly visited two plants in the gardens - *Asclepias incarnata* and *Echinacea purpurea* – and there was no significant difference in the abundance of this bee species at the two site types. In fact, if one of my garden sites did not have *Asclepias incarnata* present, I strongly suspect there would have been significantly fewer *B. griseocollis* in the gardens than the natural areas.

Some information about the life history of these bumble bees can give better context as to why these patterns likely emerged. *B. impatiens* and *B. bimaculatus* are both generalists that can

access pollen and nectar resources from flowers of all different sizes (Colla et al. 2008). They are among the group of generalist species that can tolerate or even benefit from landscape disturbances such as urban development (Goulson et al. 2008; Colla et al. 2012). *B. griseocollis* is a specialist that can't access pollen and nectar resources from all types of flowers as easily (Villalona et al. 2020). The *Asclepias incarnata* flowers were only available at one of the garden sites I visited, and this site had the vast majority of *B. griseocollis* visits that I recorded among the gardens. If homeowners and land managers alike want to encourage more visitation from *B. griseocollis*, they should provide flowers with short corollas and flowers in the *Asclepias* genus that align with this species' preference for the genus in natural areas.

The difference in the number of plant-pollinator “connections” between the two site types, as shown in Figures 6 and 7, is notable for a few reasons. It is perhaps unsurprising that bees visited the greater diversity of flowers present in the gardens, yet it is intriguing to consider the implications of greater floral diversity in terms of network resilience. Could the plant-pollinator networks in the gardens be more resilient than those in the natural areas? This is an intriguing opportunity to explore in further research.

Flowers, of course, aren't the only resource that matters to bees. Something I did not specifically measure in my study was quantity or quality of available nesting substrates. Bees have a diverse range of nesting substrate preferences from inhabiting abandoned rodent nests (bumble bees), digging a hole in bare soil (miner bees), or even cozying up in dead standing stems (small carpenter bees and leafcutter bees). It is particularly important for gardeners and homeowners to create (or simply to not destroy) potential bee nesting habitats – leaf litter, grass clumps, fallen logs, standing stems, and bare soil – since many bees do not travel very far from home to look for food. A future opportunity for research would be to measure the presence of

suitable nesting habitats and of nesting abundance in gardens compared to nearby natural areas. It is possible that my results are skewed to show more bees in gardens because of a “magnet effect” where bees from surrounding areas are attracted to the dense floral resources. The floral resources in the natural areas are more spread out and thus bees could be spread out with them. Measuring the nesting density of bees could be an interesting way to approximate bee abundance in the two areas to see if gardens still show greater bee abundance through this metric.

## **Community Impacts**

Communication and interaction with the public was a core element of my study. I worked directly with homeowners to research on their property and built personal relationships with them through the time we spent together. I created a pamphlet for these homeowners that shows the most highly visited floral species from their gardens and recommendations for how they can manage for pollinators. The Armstrong Garden site was created by and is still maintained by Williamstown’s Bee City USA Committee. I spent time with several members of the committee to provide feedback about their management practices, and I did an interview with Marty Seufer, the committee’s lead organizer, about my research (Williamstown WV 2021). I also interacted with biologists at the Ohio River Island National Wildlife Refuge (ORINWR). Elain Barr, ORINWR’s head biologist, was my primary contact. I shared the plant list from that site, my data, and results with ORINWR and with the state of West Virginia’s Department of Natural Resources.

## Acknowledgments

Thank you to my advisor, Dr. Robin Bingham, for her tireless support. Robin helped me set ambitious – yet achievable – goals for this project, kept me on track with meeting deadlines, gave feedback on presentations, read & edited numerous paper drafts, and so much more. She was incredibly patient and disciplined in the ways I needed to be successful. Thank you to my other committee members, Dr. Jennie Reithel and Dr. Tori Reynolds, for providing pertinent feedback on study design, statistical analysis, and writing. Thank you to all the property owners that let me stomp around in their backyards and fields. Robert, Molly, Kelly & Jim & Dan, Lori, Suzannah & Bruce, and Jason – I literally could not have done this project without your willingness to share your space. It was delightful getting to know each of you, and I look forward to hearing about the bees you continue to attract. Thank you to the Ohio River Islands National Wildlife Refuge and to Williamstown’s Bee City USA Committee for allowing me to work on your properties, as well. Elaine, Joyce, and Marty – your dedication to protecting wildlife and conserving green spaces is an inspiration. Thank you to CanBee Cocktails for the Anthophila Grant, Western Colorado University for the M.S. in Ecology Research Grant, and the Haley Project Fund for the Graduate Studies Grant that helped fund my studies and thesis research. A special thank you to my two impromptu research assistants, Kelly Rattray and Michael Brokensha. Kelly and Mike took turns accompanying me on site surveys, carrying the “bee cooler”, juggling other research supplies, and recording data. This work was not easy- they endured high heat and humidity, hours of the direct afternoon sun, ticks, chiggers, thorny plants, and several surprisingly strenuous walks up unassuming hills. Their help made my work faster, easier, and so much more enjoyable. Thank you!

## Literature Cited

- Ahrné, K., J. Bengtsson, and T. Elmqvist. 2009. Bumble Bees (*Bombus* spp) along a Gradient of Increasing Urbanization. *PLoS ONE* **4**:e5574.
- Bates, A. J., J. P. Sadler, D. Grundy, N. Lowe, G. Davis, D. Baker, M. Bridge, R. Freestone, D. Gardner, C. Gibson, R. Hemming, S. Howarth, S. Orridge, M. Shaw, T. Tams, and H. Young. 2014. Garden and Landscape-Scale Correlates of Moths of Differing Conservation Status: Significant Effects of Urbanization and Habitat Diversity. *PLoS ONE* **9**:e86925.
- Bushman, S.L., and F.A. Drummond. 2015. Abundance and Diversity of Wild Bees (Hymenoptera: Apoidea) Found in Lowbush Blueberry Growing Regions of Downeast Maine. *Environmental Entomology* **44**:975-989.
- Cane, J., and V. Tepedino. 2001. Causes and Extent of Declines among Native North American Invertebrate Pollinators: Detection, Evidence, and Consequences. *Conservation Ecology* **5**.
- Cameron, S.A., H.C. Lim, J.D. Lozier, M.A. Duennes, and R. Thorp. 2016. Test of the invasive pathogen hypothesis of bumble bee decline in North America. *Proceedings of the National Academy of Sciences* **113**:4386–4391.
- Cameron, S.A., J.D. Lozier, J.P. Strange, J.B. Koch, N. Cordes, L.F. Solter, and T. Griswold. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences* **108**(2):662-667.
- Colla, S.R., and L. Packer. 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. *Biodiversity and Conservation* **17**:1379.
- Colla, S.R., F. Gadallah, L. Richardson, D. Wagner, and L. Gall. 2012. Assessing declines of North American bumble bees (*Bombus* spp.) using museum specimens. *Biodiversity and Conservation* **21**:3585-3595.
- Cresswell, J.E., J.L. Osborne, and D. Goulson. 2000. An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. *Ecological Entomology* **25**:249–255.

- Fortel, L., M. Henry, L. Guilbaud, A.L. Guirao, M. Kuhlmann, H. Mouret, O. Rollin, and B.E. Vaissière. 2014. Decreasing Abundance, Increasing Diversity and Changing Structure of the Wild Bee Community (Hymenoptera: Anthophila) along an Urbanization Gradient. *PLOS ONE* **9**:e104679.
- Gerner, E. E., and R. D. Sargent. 2022. Local plant richness predicts bee abundance and diversity in a study of urban residential yards. *Basic and Applied Ecology* **58**:64–73.
- Geslin, B., B. Gauzens, E. Thébault, and I. Dajoz. 2013. Plant Pollinator Networks along a Gradient of Urbanisation. *PLOS ONE* **8**:e63421.
- Goulson, D., G.C. Lye, and B. Darvill. 2008. Decline and Conservation of Bumble Bees. *Annual Review of Entomology* **53**:191-208.
- Graystock, P., D. Goulson, and W.O.H. Hughes. 2014. The relationship between managed bees and the prevalence of parasites in bumblebees. *PeerJ* **2**:e522.
- Grixti, J.C., L.T. Wong, S.A. Cameron, and C. Favret. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. *Biological Conservation* **142**:75–84.
- Hagen, M., M. Wikelski, and W.D. Kissling. 2011. Space use of bumblebees (*Bombus* spp.) Revealed by radio-tracking. *PLOS ONE* **6**:e19997.
- Hall, D.M., G.R. Camilo, R.K. Tonietto, J. Ollerton, K. Ahrné, M. Arduser, J.S. Ascher, K.C.R. Baldock, R. Fowler, G. Frankie, D. Goulson, B. Gunnarsson, M.E. Hanley, J.I. Jackson, G. Langellotto, D. Lowenstein, E.S. Minor, S.M. Philpott, S.G. Potts, M.H. Sirohi, E.M. Spevak, G.N. Stone, and C.G. Threlfall. 2017. The city as a refuge for insect pollinators. *Conservation Biology*, **31**(1):24-29.
- Jacobson, M.M., E.M. Tucker, M.E. Mathiasson, and S.M. Rehan. 2018. Decline of bumble bees in northeastern North America, with special focus on *Bombus terricola*. *Biological Conservation* **217**:437–445.
- Kearns, C.A., and D.W. Inouye. 1997. Pollinators, Flowering Plants, and Conservation Biology. *BioScience* **47**:297–307.

- Koh, I., E.V. Lonsdorf, N.M. Williams, C. Brittain, R. Isaacs, J. Gibbs, and T.H. Ricketts. 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proceedings of the National Academy of Sciences* **113**:140–145.
- Krahner, A., J. Schmidt, M. Maixner, M. Porten, and T. Schmitt. 2021. Evaluation of four different methods for assessing bee diversity as ecological indicators of agro-ecosystems. *Ecological Indicators* **125**:107573.
- Lagucki, E., J. D. Burdine, and K. E. McCluney. 2017. Urbanization alters communities of flying arthropods in parks and gardens of a medium-sized city. *PeerJ* 5:e3620.
- Larson, J.L., A.J. Kesheimer, and D.A. Potter. 2014. Pollinator assemblages on dandelions and white clover in urban and suburban lawns. *Journal of Insect Conservation* 18:863–873.
- LeBuhn, G., T. Griswold, R. Minckley, S. Droege, T. Roulston, J. Cane, F. Parker, S. Buchmann, V. Tepedino, N. Williams, C. Kremen, and O. Messenger. 2003. A standardized method for monitoring bee populations – The Bee Inventory (BI) Plot.
- Liu, Z., C. He, Y. Zhou, and J. Wu. 2014. How much of the world’s land has been urbanized, really? A hierarchical framework for avoiding confusion. *Landscape Ecology* **29**:763–771.
- Lowenstein, D.M., K.C. Matteson, I. Xiao, A.M. Silva, and E.S. Minor. 2014. Humans, bees, and pollination services in the city: the case of Chicago, IL (USA). *Biodiversity and Conservation* 23:2857–2874.
- Lowenstein, D.M., K.C. Matteson, and E.S. Minor. 2019. Evaluating the dependence of urban pollinators on ornamental, non-native, and ‘weedy’ floral resources. *Urban Ecosystems* 22:293–302.
- Majewska, A.A., S. Sims, S.J. Wenger, A.K. Davis, and S. Altizer. 2018. Do characteristics of pollinator-friendly gardens predict the diversity, abundance, and reproduction of butterflies? *Insect Conservation Diversity* **11**:370-382.
- Mallinger, R.E., P. Werts, and C. Gratton. 2015. Pesticide use within a pollinator-dependent crop has negative effects on the abundance and species richness of sweat bees, *Lasioglossum* spp., and on bumble bee colony growth. *Journal of Insect Conservation* **19**:999-1010.



- Martins, K.T., A. Gonzalez, and M.J. Lechowicz. 2017. Patterns of pollinator turnover and increasing diversity associated with urban habitats. *Urban Ecosystems* 20:1359–1371.
- Théodore Munyuli, M.B. 2012. Is pan-trapping the most reliable sampling method for measuring and monitoring bee biodiversity in agroforestry systems in sub-Saharan Africa? *International Journal of Tropical Insect Science* 33:14–37.
- Osborne, J.L., S.J. Clark, R.J. Morris, I.H. Williams, J.R. Riley, A.D. Smith, D.R. Reynolds, and A.S. Edwards. 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology* 36:519–533
- R Core Team. R: A language and environment for statistical computing. 2021. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Samuelson, A.E., R.J. Gill, M.J.F. Brown, and E. Leadbeater. 2018. Lower bumblebee colony reproductive success in agricultural compared with urban environments. *Proceedings of the Royal Society B: Biological Sciences* 285:20180807.
- Sirois-Delisle, C., and J.T. Kerr. 2018. Climate change-driven range losses among bumblebee species are poised to accelerate. *Scientific Reports* 8:14464.
- Steffan-Dewenter, I. 2002. Landscape context affects trap-nesting bees, wasps, and their natural enemies. *Ecological Entomology* 27:631–637.
- Verboven, H.A.F., R. Uyttenbroeck, R. Brys, and M. Hermy. 2014. Different responses of bees and hoverflies to land use in an urban–rural gradient show the importance of the nature of the rural land use. *Landscape and Urban Planning* 126:31–41.
- Villalona, E., B.D. Ezray, E. Laveaga, A.A. Agrawal, J.G. Ali, and H.M. Hines. 2020. The role of toxic nectar secondary compounds in driving differential bumble bee preferences for milkweed flowers. *Oecologia* 193:619–630.
- Weather averages Williamstown, West Virginia. (n.d.).  
<https://www.usclimatedata.com/climate/williamstown/west-virginia/united-states/uswv1487>.

- Wenzel, A., I. Grass, V.V. Belavadi, and T. Tschardt. 2020. How urbanization is driving pollinator diversity and pollination – A systematic review. *Biological Conservation* **241**:108321.
- Westphal, C., R. Bommarco, G. Carré, E. Lamborn, N. Morison, T. Petanidou, S.G. Potts, S.P.M. Roberts, H. Szentgyörgyi, T. Tscheulin, B.E. Vaissière, M. Woyciechowski, J.C. Biesmeijer, W.E. Kunin, J. Settele, and I. Steffan-Dewenter. 2008. Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs* **78**(4):653-671.
- Williamstown WV. 2021. Bee City Interview - 07/12/2021. URL <https://www.youtube.com/watch?v=daeyhbwaZNQ>.
- Wood, T.J., J. Gibbs, K.K. Graham, and R. Isaacs. 2019. Narrow pollen diets are associated with declining Midwestern bumble bee species. *Ecology* **100**:e02697.
- Woodard, S.H., S. Federman, R.R. James, B.N. Danforth, T.L. Griswold, D. Inouye, Q.S. McFrederick, L. Morandin, D.L. Paul, E. Sellers, J.P. Strange, M. Vaughan, N.M. Williams, M.G. Branstetter, C.T. Burns, J. Cane, A.B. Cariveau, D.P. Cariveau, A. Childers, C. Childers, D.L. Cox-Foster, E.C. Evans, K.K. Graham, K. Hackett, K.T. Huntzinger, R.E. Irwin, S. Jha, S. Lawson, C. Liang, M.M. López-Urbe, A. Melathopoulos, H.M.C. Moylett, C.R.V. Otto, L.C. Ponisio, L.L. Richardson, R. Rose, R. Singh, and W. Wehling. 2020. Towards a U.S. national program for monitoring native bees. *Biological Conservation* **252**:108821.
- Zattara, E.E., and M.A. Aizen. 2021. Worldwide occurrence records suggest a global decline in bee species richness. *One Earth* **4**:114-123.