EFFECTS OF ABUNDANCE, DIVERSITY, AND HEALTH OF NATIVE POLLINATORS IN URBAN FOREST FRAGMENTS

by

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A thesis submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Master of Science in Entomology

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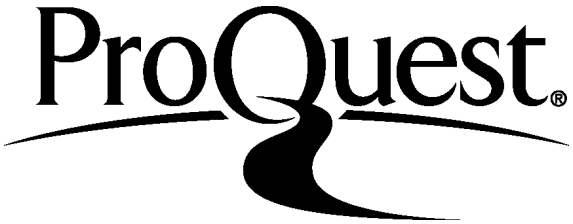

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ABSTRACT

Bees are essential for crop pollination services; however, the ecosystem services they provide by pollinating native plants are crucial for maintaining biodiversity in natural systems. This study analyzed bee community changes within, on the edge, and outside of forest fragments. Phenological variation over two seasons and modeling to predict bee abundance associated with forest characteristics was performed. Finally the genetic diversity of two species of *Bombus* was analyzed. Bowl traps and aerial sweep netting in and near forest patches were used to sample bee communities in northern Delaware between March and August, 2013 and 2014. Bee phenology stayed consistent between field seasons, but fewer bees were collected in 2014 compared to 2013. Abundance modeling (R: unmarked) predicted that bee abundance was negatively impacted primarily by agriculture surrounding the forest patch. Analyses using microsatellites revealed that *B. impatiens* lacked overt population genetic structure while *B. bimaculatus* showed two genetically distinct populations. Pesticide analysis revealed 17 pesticides observed on adult bees from seven urban and suburban forest patches. Further studies investigating natural bee fluctuations in response to multiple field seasons, floral diversity, and chronic pesticide exposure are crucial in order to assess native pollinator health.

Chapter 1

EFFECTS OF ABUNDANCE, DIVERSITY, AND HEALTH OF NATIVE POLLINATORS IN URBAN FOREST FRAGMENTS

1.1 Introduction

Bees provide ecosystems with pollination services in all types of environments; 67% of all flowering plants depend on insects for pollination (Suttle 2003). Ninety percent of angiosperms are reliant on biotic pollination for reproduction and maintenance of genetic viability, where crop plants represent less than 0.1% of angiosperm species globally (Menz *et al.,* 2011), demonstrating that most relationships between plants and insects are challenging to assess in terms of an economic value. Although honey bees (*Apis mellifera* L.) are the primary pollinators used in agricultural systems (valued at over $14 billion in the US and over $215 billion worldwide (van Engelsdorp *et al.,* 2008)), native bees are being recognized for their pollination efficiency and specialized foraging behavior. The value of alfalfa attributed to pollination by *Megachile rotundata* F. (the alfalfa leafcutter bee) falls between $5 - $7 US billion (Calderone, 2012). In a time where humans are intensely modifying the landscape, habitat degradation, loss, and fragmentation can cause huge declines in plant and/or pollinator populations and disrupt mutualistic relationships that have developed over an evolutionary timescale (Menz *et al.,* 2011).

1.1.1 Pollinator importance and decline

Pollinator decline and shifts in abundance have been documented throughout the managed bee community; however, assessments of non-managed bee declines are more challenging to observe. Honey bee colonies have suffered high winter losses, particularly between 2007-2010 (van Engelsdorp *et al.,* 2008, 2010). *Bombus* species have seen a steep decline over the past 140 years compared to other native bee species (Bartomeus *et al.,* 2013), and over the same time period large shifts in pollinator community structure have been observed in the northeastern United States (Evans *et al*., 2008). Colony losses of 4-5% annually have been reported in other managed bees such as Mayan stingless bees (Villanueva-Guiterrez *et al.,* 2013); however, the true loss of non-managed bee species is generally underestimated and overlooked.

1.1.2 Pollinator diversity and behavior

Bees are a diverse group of insects, with over 20,000 species of native bees (superfamily Apoidea) described in the world (Michener *et al*., 2007). Eusociality in insects is broadly defined as having cooperative brood care, overlapping generations, and a reproductive division of labor. Nearly 99% of bees are solitary, where they do not live in a colony and one individual is responsible for provisioning for its own developing brood. In the United States, almost all bees are solitary with the exception of bumble bees (*Bombus* spp.), which live in ground-dwelling colonies, and a few species in the family Halictidae. Some native bees tend to live gregariously but this behavior has been linked to the exploitation of favorable resources such as nesting substrate, and does not meet eusocial behavior criterion.

Most bees are specialists or oligolectic pollinators, meaning they specialize on closely related species or a genus of flowering plants. Generalist pollinators, such as

bumble bees, collect pollen and nectar from multiple genera or species of flowers. Specialists have developed a close relationship with the flowers that they visit, and are extremely sensitive to loss of both biodiversity and habitat since their floral resource may be limited in its distribution.

Generalist pollinators exploit high resource patches much more effectively than solitary bees, simply by virtue of their foraging behavior (Morales and Aizen 2006). Bees such as *Apis mellifera* require a diversity and large quantity of rewarding and resourceful flowers to maintain their large hives and to store enough honey to overwinter efficiently; therefore, they will search for over 10 km for the most abundant flower source (Graham 1992). Most solitary bee species do not overwinter, so finding the most resource-rich flower is unnecessary.

Solitary bees have a foraging distance of 150 m – 600 m from the nesting site to food patches (Gathmann 2002). Differences in resource use by native bees is further demarcated by the fact that far apart forest fragments typically hinder smaller bees from traveling between them, and larger bees tend to be capable of moving between fragments, although this depends on the bee's life history (Tonhasca *et al.,* 2003).

1.1.3 Factors influencing pollinator health

Pollinator decline in lieu of pesticide exposure has been a major focus of pollination ecology research in the past decade, suggesting that certain pesticides can have devastating impacts on pollinator survivorship (Mullin *et al,*. 2010; Johnson *et al.,* 2010; van Engelsdorp *et al.,* 2008). Over 200 pesticide residues have been found in managed honey bee hive matrices such as pollen, wax, and the bees themselves. Pesticides have also been shown to heavily impact the native bee community. *Osmia lignaria* Say, a managed native leafcutter bee, displayed signs of high mortality due to

phosmet exposure (Alston *et al*., 2007) and a period of inactivity for a few hours after exposure to Rovral, Dyne-Amic, and Bayfolan Plus (Ladurner *et al*., 2008). Effects of pesticide exposure may vary between bee species and the type of pesticide used. Sprays of Imidacloprid had no effect on colony vitality or worker behavior in *Bombus impatiens* Cresson; however, exposure to chlorpyrifos, carbaryl, and cyfluthrin negatively impacted colony vitality (Gels *et al*., 2002). For the leafcutter bee *Osmia bicornus* L, sublethal pesticide exposure resulted in an approximately 50% reduction in total offspring production, created a significantly male-biased sex ratio in offspring, and did not increase adult bee mortality (Sandrock *et al*., 2014). Interactions with bees and pesticides may not just impact adults but could have devastating impacts on developing brood, which are often bathed in food that may contain mixtures of various chemistries.

Pollinator health is directly tied to available forage and nectar; however, pollen in particular is a key component of bee development. Pollen is the main protein source for developing larval bees, and larval development tends to vary depending on both the pollen type, and more specifically, the nutritional composition of the pollen. Pollen diet is a crucial factor in the development of viable brood for all pollinators; therefore, the nutrition and variety of flower types determines the health of bees. Generalist bees have shown preferential pollen collecting behavior, but foraging choices may not be limited to a specific family or genus of plants (Saifuddin and Jha, 2014) and nutritional value of individual plant taxa has not been directly linked to pollinator preference. It has been demonstrated that some individuals cannot develop from just one species of pollen and need a heterogeneous mixture (Haider *et al.,* 2013; Eckhardt *et al.,* 2014).

Studies have also shown that the loss of important forage can result in the decline of an associated pollinator. In Britain the decline in bumble bee populations was correlated to a 76% reduction in available forage (Carvell *et al.,* 2006). It is important for bees to have access to the most appropriate pollen sources for development; therefore, bees tend to be more selective and restrictive in their pollen source choice compared to nectar sources (the main carbohydrate source) (Cane and Sipes, 2006; Wcislo and Cane, 1996). These preferences possibly stem from larval physiological limitations and/or adaptations to digesting specific pollen species (Mueller and Kuhlmann, 2008; Sedivy *et al.,* 2011, 2013). Fortunately, bees can switch to non-native plants for pollen, and studies have documented that some native bees collect pollen from non-native plants (Hinners and Hjelmroos-Koski, 2009). This plasticity is beneficial if native plants are absent due to competition with non-native plants. However, the interaction between native bees and non-native plants can have negative impacts on the reproductive success of native plants in the ecosystem. Many urban landscapes provide non-native floral resources for pollinators throughout the summer, but the fitness of bees developing on non-native pollen types is not known.

1.1.4 Population genetics

One method of assessing population health is by analyzing the genetic diversity of individuals within and between different populations in a species. Studies on honey bees have demonstrated that an increase in genetic diversity at the colony level is correlated with disease resistance (Seeley and Tarpy, 2007), increased foraging productivity (Mattila and Seeley, 2007), and an increase in resource communication signals between workers (Mattila *et al.,* 2008). Social pollinators such as bumble bees

may also be negatively affected by losses in genetic diversity which may confer to a decrease in disease resistance.

In order to assess genetic diversity, genetic markers such as microsatellites can be used to determine differences population genetics. Microsatellites are tandem repeats of usually 1-6 base pairs which are distributed consistently and evenly at many different genomic loci (Kantartzi, 2013). These simple sequence repeats (SSRs) are highly variable in the number of repeat units among individuals and populations. Microsatellites are popular in the genetic field because of their codominant and polymorphic nature between closely related lines and also because they require small amounts of DNA. Microsatellites can be highly polymorphic and provide good estimates of heterozygosity even in social insects, which makes them ideal markers for genetic variability studies for bees (Queller *et al.,* 1993). Lower genetic diversity would indicate that populations have either gone through a bottleneck, founder event, and/or the population has been isolated from other populations, thereby resulting in reduced gene flow.

Lozier *et al.* (2011) found that populations of declining bumble bee species had reduced levels of genetic diversity, and island populations in particular exhibited strong genetic drift, suggesting that isolated populations in any environment could have resultant low genetic variation. Therefore, bee species, theoretically, could have strikingly different levels of gene flow in fragmented habitats (Suni and Brosi 2012). Some species such as honey bees mate with multiple individuals (polyandry) in order to increase the genetic diversity of their offspring (Payne *et al.,* 2003); however, this advantage is not seen in many native bee species.

Genetically threatened bees typically have populations with fewer individuals and suffer from high extinction risk. A reduction in population size can lead to the reduction in the number of occupied patches over time. Extinction rates have been shown to be strongly dependent both on local bee population size and patch habitat quality (Franzén and Nilsson 2010). Therefore, fragmented landscapes with patchy forage distribution could lead to losses in genetic diversity within different bee species.

1.1.5 Landscape effects on pollinators

Habitat loss and the invasion of non-native species are considered some of the main causes of species loss (Wilcove *et al.,* 1998). Habitat loss or fragmentation can lead to the invasion of exotic competitors or predators, reduced immigration, disturbance in the surrounding matrix, edge effects, changes in community structure, and reduced population sizes (Cane and Sipes, 2006).

Invasive species occur globally, and can have a large impact especially in forest fragments, disrupting mutualistic relationships between native plants and pollinators. Highly invaded webs exhibit weaker mutualistic relationships between plants and animals than less-invaded webs, and these mutualisms are asymmetric, where the plants are more reliant on the animals (Aizen *et al*., 2008). Invasive species can also cause an increase in asymmetric interactions during advanced stages of invasion since most invasive species tend to attract generalists (Aizen *et al*., 2008). This results in more pollinator species becoming dependent on the invasive plant species, which alters the native pollinator's relationship with native plant taxa, diminishing pollinator interactions with native plants (Aizen *et al.*, 2008). Interactions between native bees and nonnative plants was explored in a study on non-native

Carpobrotus acinaciformis (L.) L Bolus and *Opuntia stricta* (Haw.) Haw. in Spain. Researchers found that *Carpobrotus acinaciformis* and *Opuntia stricta* were visited by 43% and 31% respectively, of all insect taxa in the ecosystem, most of which were native insects (Bartomeus *et al.*, 2008; Olesen *et al.,* 2008). Typically, generalist pollinators visit both native and non-native plants; however, oligolectic bees have been documented visiting non-native plants, which could pose a threat to specialist interactions and the extinction of native plant taxa (Bartomeus *et al.,* 2008; Hinners and Hjelmroos-Koski, 2009).

Forest fragmentation has been seen to negatively impact native plant germination more so than non-native plant germination, which further amplifies the competitive abilities of non-native plants (Ashworth and Marti, 2011). *Rosa multiflora* Thunb., a common invasive shrub, utilizes generalist insect pollinators, and in general, many invasive plants tend to have showy inflorescences or high nectar rewards, which could potentially allow them to outcompete native plants (Jesse *et al.,* 2006).

1.1.6 Reliance on native bees

Native bees species may become increasingly important to farmers in larger field settings (Lonsdorf *et al.,* 2009). Currently, farmers rely heavily on managed pollinators such as honey bees, bumble bees, and mason bees, which worldwide constitute only 11 of the 20,000 – 30,000 species of bees (Kremen *et al.,* 2002). In agricultural systems, many *Bombus* species are more efficient at pollinating poricidal dehiscent crops such as blueberries, peppers, and tomatoes due to unique pollination behaviors exhibited by species such as bumble bees that sonicate or buzz pollinate the flowers releasing the sticky pollen (Winfree *et al,.* 2007; Lonsdorf *et al.,* 2009).

Additionally, native bee communities are thought to provide an insurance policy in the case of honey bee shortages (Kremen *et al.,* 2002). Native pollinators provide significant pollination to native plants in specifically formed webs in unmanaged as well as agricultural habitats. Diverse wild-bee communities have been shown to enhance the stability, quality, and quantity of pollination services compared with the reliance of a single, managed species (Lonsdorf *et al.,* 2009). Wild bees have also been shown to provide sufficient pollination to agricultural crops such as watermelon and pumpkin (Kremen *et al.,* 2002; Julier and Roulston 2009). Key factors to their success in pollination include the availability of nesting sites in varying substrates (stems, twigs, pith, and dirt) and proximity of nesting sites to crops (Ricketts 2004; Lonsdorf *et al.,* 2009; Bailey *et al.,* 2014). Previous research has focused on agricultural and natural systems such as meadows; however, little is known about the true value of the ecosystem services bees provide to forest landscapes.

1.1.7 Foraging behavior

Bee foraging behavior differs depending on the community, size, availability, and distance of the foraging area, and also differs depending on the species. Although solitary bees are found to have small foraging ranges, local habitat structure appeared to be more important than larger-scale landscape structure (Gathmann 2002). Foraging abilities vary depending on the species; different life histories allow some bees to prefer pastures where other bees prefer forested patches (Brosi *et al.,* 2008). Certain bees also have lower species richness in more stable forests and prefer secondary or disturbed sites, possibly due to a higher plant diversity (Brosi *et al.,* 2008). In a study by Gathmann and colleagues (1994), younger fields were colonized first by large trap-

nesting bees, whereas older fields were colonized first by small bees, indicating that species community may vary depending on the successional status of the landscape.

Flower handling can also vary depending on the life history of the bee species. Munyuli (2014) found that solitary bees foraged on more flowers per foraging trip than social bees, but spent less time per flower visited. Additionally, solitary bees, in a study on coffee trees, visited more coffee trees but deposited less pollen, whereas social bees visited fewer trees but deposited more pollen on flowers (Munyuli 2014). Due to bees having a varied foraging range, certain bees may be impacted by spatial distance more than others. Various studies showed that native bee brood production was negatively impacted by greater spatial separation of nesting and floral resources (Zurbuchen *et al*., 2010; Schnitzler *et al.,* 2011), further implying that native pollinators tend to nest close to floral resources.

1.1.8 Abundance and diversity

Species diversity in native bee communities also contributes to the pollination and reproduction of plants in natural and agricultural habitats (Winfree *et al.,* 2007; Hoehn *et al.,* 2008). Agricultural fields and suburban and urban developments have been shown to have high bee abundance and species richness compared to extensive evergreen forests. Plant composition not only in the foraging habitat but also in the surrounding landscape has a positive impact on native pollinators (Steffan-Dewenter et al. 2002; Carvell *et al*., 2006; Wojcik *et al.,* 2008) supporting the notion that plant diversity throughout a landscape is important. Potts and colleagues (2003) demonstrated that bees responded positively to natural disturbances such as forest fires, and other studies have shown that native bees are able to persist in human-made disturbed areas (Winfree *et al.,* 2007). Wild pollinators have also been shown to

decrease in abundance with an increase in isolation from natural habitats in certain ecosystems such as chaparral, tropical moist, subtropical dry, and subtropical premontane forests (Winfree *et al.,* 2007).

Many pollinators are found in disturbed areas due to the abundance of floral resources and nesting areas; however, most research on bees focuses on richness and diversity in forest edges, disturbed areas, and fields, but the importance of pollinators found inside temperate deciduous forest fragments is just beginning to be explored.

Overall, bee communities are structured in a way that is dependent on the local floral resources and available nesting substrates (Brosi *et al.,* 2008). Smaller, cavity nesting bees tend to be localized in more disturbed and smaller fragments where larger ground nesting bees are more common in larger and less disturbed fragments (Cane and Sipes, 2006; Wray *et al.,* 2014).

Bee abundance has been shown to increase with increasing fragment size and decreasing isolation, whereas species richness was positively correlated with increasing edge effects and negatively correlated with fragment area (Brosi *et al.,* 2008). Abundance and richness has also been shown to decrease with an increasing distance to forest edge habitats (Bailey *et al.,* 2014), suggesting that these forest edges play a key role in pollinator habitats, but the role of interior forest for pollinator habitat is still relatively unknown in deciduous forests.

1.1.9 Significance and rationale

The assessment of pollinator health and proliferation in deciduous urban forest fragments in the Mid-Atlantic is not well documented. Urban forest fragmentation is increasing at an alarming rate as human expansion and development increases across the landscape. Prior research on bee abundance and community structure showed that

the percent impervious surface negatively impacted native bee communities, and surrounding forest cover positively influenced native bee communities (Taki *et al.,* 2007; Fortel *et al.,* 2014). These relationships can likely be explained by the bees' dependence on nesting availability and flower resources within forest fragments, agriculture, suburban, and urban landscapes.

Forest fragmentation may impact pollinators directly by limiting their available resources; however, these pollinators are also likely impacted by indirect effects of habitat fragmentation such as an increase in exposure to pesticides in an urban landscape. With the detection of numerous chemistries in managed bee matrices and the unknown impacts these chemical cocktails are having on our managed pollinator force, it is crucial to understand the impact of pesticide exposure to wild bees utilizing resources in various habitat types. Although bees provide essential ecosystem services within forest edges and agriculture, their role in urban forest fragments surrounded by a varying landscape is unknown, and risks to pollinators in these human dominated systems have not been established.

This study focuses on the density and success of wild bees in urban forests in the Mid-Atlantic in response to pesticide exposure and habitat fragmentation. This study specifically aims to understand the temporal stability of pollinator populations and the affect forest fragmentation has on the genetic integrity of these populations. The importance of the ecosystem services provided by native bee populations is well established; populations can serve not only as an insurance policy for declining managed bees but more importantly as the sole pollinators for many native plants. The goal of this project is to assess wild bee diversity and health in urban forest fragments in the Mid-Atlantic.

1.1.10 Hypotheses

Our first hypothesis is that forest fragmentation impacts native bee abundance and richness. We predict that forest fragmentation will negatively impact pollinator abundance, richness, and diversity. In particular, we hypothesize that an increase in agriculture and impervious surface surrounding forest fragments will decrease richness, diversity, and abundance while patch size will increase these indices. We predict that certain forest characteristics such as soil saturation and nonnative stem mass will have a negative effect on bee abundance, diversity, and richness. We also predict that site characteristics such as native stem mass, understory density, tree density, organic matter in soil, and leaf litter volume will have a positive effect on bee diversity, abundance, and richness. Our second hypothesis is that forest fragmentation impacts the population genetics of bumble bees. We predict forest fragmentation to have a negative impact on the genetic structure, particularly in *Bombus* species. *Bombus* species are predicted to have genetically separate populations based on geographic and fragment isolation, where isolated forest fragments harbor isolated *Bombus* populations which would have lower genetic diversity due to lack of gene flow.

1.1.11 Specific objectives

- To survey and collect wild bees and develop a database as a reference
- To measure the abundance and diversity of wild bee species in fragments
- To assess pesticide levels in pollinators collected from forest fragments
- To correlate land use activities with pesticide exposure
- To measure the genetic diversity of select bee populations
- To develop an assessment program for outreach and extension materials

1.2 Methods

A pilot field season was conducted from mid-June through early September 2012. Investigative field seasons were conducted beginning mid-March through mid-October 2013 and through mid-July 2014. Areas of focus in the field research included collecting small bees with bowl traps, collecting large bees with aerial nets, and collecting flower samples throughout each field site.

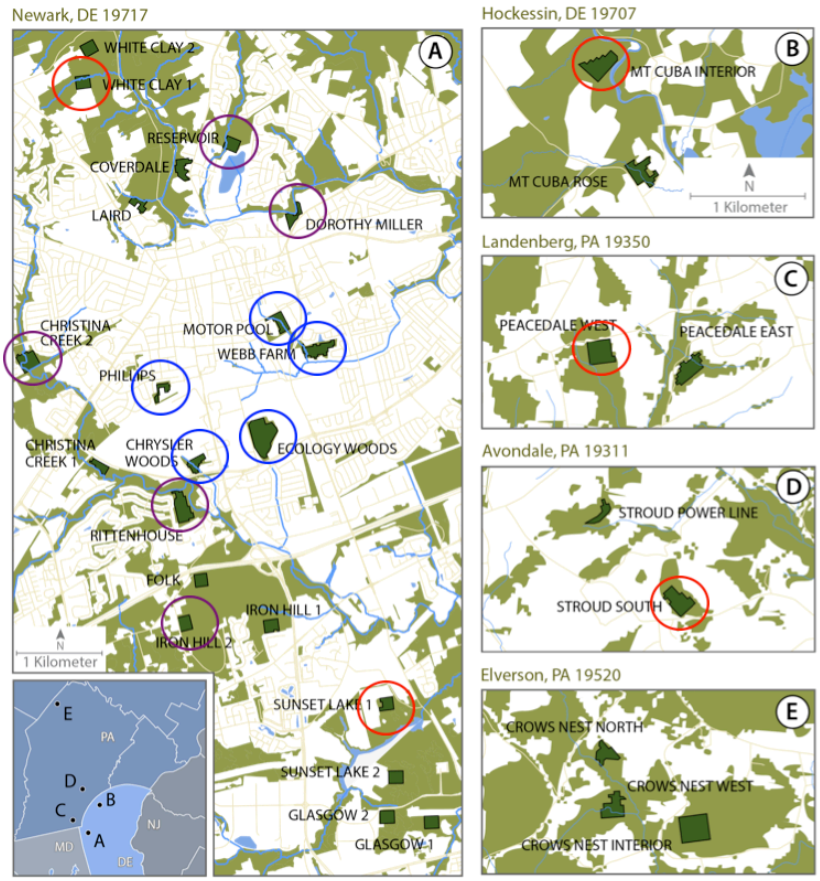
1.2.1 Field sites

Field sites were established prior to all field seasons and are part of the Forest Fragments in Managed Ecosystems (FRAME) project in the Department of Entomology and Wildlife Ecology. FRAME is designed as a long-term monitoring project on the succession of urban and suburban forest fragments. The FRAME project includes occupancy and abundance of Cerambicidae beetles, diversity of terrestrial arthropods, monitoring of Wood Thrush and Gray Catbird populations, forest health observed by measuring forest cover, percent of understory invaded by *Rosa multiflora*, surrounding landscape use, and other variables.

FRAME field sites are representative of typical forest fragments in the Mid-Atlantic region as plots of forest surrounded by developed land such as suburban housing, agriculture, urban sprawl, and roadways (Figure 1.1). In addition, many sites are particularly isolated from other forest fragments and some have been isolated for decades. Each FRAME field site has been marked and flagged at 25 m intervals using GPS units, and points are labeled with sequential letters and numbers. At least 10 randomly selected points within each site were chosen to gather point-collected data (soil, leaf litter, etc.). Other variables such as surrounding landscape composition and

percent nonnative cover are site-wide variables as opposed to point-based (Rega, 2012)

Figure 1.1: Locations of all FRAME field sites in northern Delaware and southeastern Pennsylvania (Vincent D'Amico, personal communication). Sites circled in blue are located in urban areas, purple are located in suburban areas, and red are located in rural/forested areas. Site sizes range from 2-16 hectares.



Field sites selected for this field research included five urban sites (Chrysler Woods, Ecology Woods, Philips, Motorpool, Webb Farm), five suburban or semi-

rural sites (Christina Creek 2, Dorothy Miller, Iron Hill 2, Reservoir, Rittenhouse), and five forested sites (White Clay 1, Mount Cuba Interior, Peacedale West, Stroud South, Sunset Lake 1) totaling 15 sites. One forested field site, Stroud South, after completing the 2013 field season, yielded almost zero bowl trap specimens due to high vandalism rates; therefore, was removed from the 2014 field season leaving 14 viable field sites. Five active points were selected in each site, and although points were randomly selected, emphasis was made in selecting points that encompassed the depth of the site (Table 1.1). At least two points were selected near the edge habitat of the site, two were selected close to the interior of the site, and one point was selected at random, totaling five points in each site.

Table 1.1: Fourteen field sites with five corresponding points and their coordinates in Universal Transverse Mercator (UTM) format.

Site	Abbreviation	Point	UTM.x	UTM.y
Christina Creek 2	CC2	E5	433071.9323	4392061.802
		F11	432940.9866	4391984.588
		G3	433136.539	4392033.123
		I11	432967.9329	4391914.624
		K9	433032.5396	4391885.946
Chrysler Woods	CW	A3	435054.1751	4390271.851
		C1	435084.3103	4390335.791
		G5	435212.1905	4390275.521
		I1	435225.4231	4390386.499
		I5	435165.5457	4390287.086
Dorothy Miller	DM	A1	436892.7884	4393319.319
		A7	436876.9942	4393468.432
		C5	436931.9631	4393423.992
		G9	437020.842	4393533.93
		I11	437065.2815	4393588.899
Ecology Woods	EW	A3	435974.8725	4390672.898
		E3	436093.7619	4390455.505
		E7	436157.3036	4390693.912
		C8	436179.269	4390513.139
		I5	436346.4526	4390622.707
Iron Hill 2	IH2	A5	434640.3286	4388107.403
		C1	434700.6407	4388013.309
		C5	434690.0285	4388112.709

		C9	434679.4163	4388212.109
		E3	434745.0345	4388068.315
Motorpool	MP	G1	444746.8305	4404707.551
		G7	444649.8305	4404821.896
		I3	444790.727	4404810.333
		K3	444796.5085	4404880.781
		K5	444899.2901	4404836.884
Mount Cuba Interior	MCI	C4	436525.9379	4392186.786
		C10	436577.792	4392046.091
		G8	436590.121	4392157.172
		I6	436637.0195	4392174.457
		K10	436654.3042	4392127.558
Peacedale West	PDW	C7	427617.9363	4400092.892
		E1	427668.6157	4400242.606
		E5	427668.1509	4400142.642
		G7	427717.7844	4400092.321
		I3	427768.3475	4400192.159
Phillips	PH	A2	434931.7114	4391444.905
		A4	434881.7296	4391445.137
		C2	434931.4793	4391394.923
		C4	434881.4975	4391395.155
		E4	434881.2655	4391345.173
Reservoir	RE	C9	436192.4263	4394680.514
		E5	436253.824	4394587.126
		G3	436271.9849	4394518.813
		G5	436228.7481	4394543.889
		G9	436142.2744	4394594.041
Rittenhouse	RH	B9	435007.8368	4389717.177
		D7	434962.8342	4389662.668
		F7	434913.0784	4389657.915
		Hi	434877.5822	4389503.894
		JI	434827.8264	4389499.141
Sunset Lake 1	SL1	A2	437260.5032	4386721.867
		A8	437410.2164	4386671.19
		C2	437310.2531	4386671.654
		C6	437360.0029	4386621.44
		E4	434309.5271	4395638.755
Webb Farm	WF	B4	434409.4908	4395638.29
		B6	434259.7775	4395688.969
		F6	434409.9552	4395738.254
		F8	434310.2238	4395788.7
		L2	436873.234	4391655.585
White Clay 1	WC1	A4	436873.002	4391605.604
		A8	436972.9654	4391605.139
		C2	436972.7333	4391555.158
		E8	437123.3746	4391704.407
		G4	433071.9323	4392061.802

1.2.2 Bowl trap samples

Bowl trap protocol was based on methods developed by Sam Droege (Droege *et al.,* 2010). Bowl traps consisted of three 3.5 oz. Solo™ bowls painted blue, yellow, or left the original white color. The different colors of the bowl traps were used to attract different pollinators. Bowl traps were filled with a propylene glycol mixture including a small amount (1tsp per gallon of glycol) of bleach to remove the color from the glycol and act as a preservative, and a small amount (2tsp per gallon of glycol) of Dawn™ dish soap (to change the viscosity and surface tension of the mixture, which allow insects to sink to the bottom of the bowl when coming into contact with the mixture).

Bowl traps were placed at five active points in 15 field sites in 2013 and 14 sites in 2014. Bowl traps were sampled from mid-March through July 2013 and 2014 as the canopy cover closed and bees were not found in these traps. All bowls were filtered for insects and the mixture replaced every two weeks. Insects were sight identified to order and anything from the order Hymenoptera (or anything unable to be sight identified) was collected into 50 ml falcon tube vials filled with 75% ethanol. Bowl traps were scored based on having Hymenopteran insects present (1), having insects present not including Hymenoptera (0), or sample vandalized (-). Vandalism was defined as bowls being broken, tipped over, emptied, or missing.

Bowl trap specimens were rinsed with water, placed in a bucket of soapy water, and separately mixed on an orbital shaker for 10 minutes. Samples were then rinsed with water and placed between two polyvinyl chloride tubes connected by a joint with a veil sealed to each end allowing air to flow through the entire tubing section. Samples were dried using a blow dryer pointed into the tubing in order to preserve museum quality bee samples (Droege *et al.,* 2010). Samples were dried, pinned and

mounted with an insect label. Labeled insects were separated between bees and wasps. Wasps were identified to the family level and bees were identified to the species level using DiscoverLife.com. To test differences in phenology over years and genera, collection events were organized as follows: Collection 1: First two weeks in April; Collection 2: Second two weeks in April; Collection 3: First two weeks in May; Collection 4: Second two weeks in May; Collection 5: First two weeks in June; Collection 6: Second two weeks in June. All scientific name authorship is provided in Table 1.25.

1.2.3 Aerial net samples

Sweep net transects were performed at every site visit beginning mid-March 2013 and 2014. Transects were performed through mid-October 2013 and early August 2014 to capture seasonal fluctuations with pollinators and flowers. Transects were determined by locating floral sources and sweeping any pollinators visiting the flowers. Transects were sweep netted at three separate locations at each site: in the interior of the site, on the edge of the site, and in the exterior of the site (10 – 50m from edge). Each transect was sampled for thirty minutes by target capturing, and all insect samples were collected into empty Falcon tube vials and stored at -80 ºC.

Sweep netted insects were separated by order, and only insects in the order Hymenoptera were stored. Samples were identified to species and photographed as part of the insect database. Insects were then kept in storage at -80 ºC for pesticide, pollen, and genetic analyses. Samples from both bowl trapping and sweep netting were identified first to order, then only samples from the order Hymenoptera were kept. All Hymenopteran samples in the superfamily Apoidea (except Sphecid wasps) were identified to species using DiscoverLife.com.

1.2.4 Flower samples and pollen analysis

Flower samples (that the pollinator was visiting) were collected into 5in x 7in glassine envelopes and a photograph of every flower was taken. Flower photographs were used to identify the flower to species if possible. Flower samples were stored and used to build a pollen reference library. Pollen was removed from each stored flower sample, dyed with fuchsin stain solution mixed with water, and pollen grains were identified and photographed with a compound microscope. Pollen photographs were maintained and uploaded to a pollen database for a developing pollen library associated with DiscoverLife.

Figure 1.2: *Hibiscus moscheutos* L. collected after a bee was seen visiting, field site Phillips (PH).

1.2.5 Pesticide analysis

Pooled bee specimens from both field seasons were separated by field site and stored at -80 ºC for pesticide analysis. Seven field sites had sufficient bee mass (3.5g) to test for over 200 pesticides and included bees from the genera *Andrena, Bombus,*

Ceratina, Lasioglossum, Megachile, Nomada, and *Osmia.* Samples were sent to Dr. Da Chen at Southern Illinois University Carbondale to test for pesticide exposure by tissue extraction.

1.2.6 Genetic analysis

Specimens stored for genetic analysis included the two most common *Bombus* species (*B. bimaculatus* Cresson and *B. impatiens* Cresson). One leg was removed from each specimen, crushed, and DNA was extracted using the DNAeasy Blood and Tissue Kit from Qiagen™. Known *Bombus* species microsatellite markers were acquired (James Strange, personal communication; Table 1.18) and amplified using Polymerase Chain Reaction, and run on a Perkin-Elmer ABI Prism™ 3730XL127 automated capillary DNA Sequencer at the Delaware Biotechnology Institute. Allele sizes were scored using the software Genemapper version 3.7 and allelic data was used for population genetic analyses.

1.2.6.1 DNA Extraction

To extract and purify DNA from *Bombus* spp., individual legs were removed from each bee, cut into four pieces, and placed in 2 ml microcentrifuge tubes. 180 µl of tissue lysis buffer (Buffer ATL) and 20 µl of proteinase K were added to each sample then mixed using a vortex mixer for 15 seconds. Once mixed, samples were placed in a water bath incubator at 56 ºC overnight. Samples were then removed and vortexed for 15 seconds, and 200 µl lysis buffer (Buffer AL) was added to each sample, then mixed by vortexing. 200 µl of 100% ethanol was then added to each sample and vortexed to mix. Precipitates along with the lysis buffer and ethanol mixture were then extracted and placed into DNeasy mini-spin columns which were

then placed into 2 ml microcentrifuge tubes. All samples were centrifuged at 8,000 rpm for 1 minute. Samples inside the mini-spin columns were removed from the 2 ml microcentrifuge tubes (which were discarded) and placed in new 2 ml microcentrifuge tubes. 500 µl of wash buffer (Buffer AW1) were added to samples and centrifuged for 1 minute at 8,000 rmp. Remaining precipitate in the microcentrifuge tubes was discarded, and the mini-spin columns were placed in new microcentrifuge tubes, 500 µl of wash buffer (Buffer AW2) were added and samples were centrifuged for 3 minutes at 14,000 rmp. The mini-spin columns were then removed from the microcentrifuge tubes (which were discarded), placed in new microcentrifuge tubes, 200 µl of elution buffer (Buffer AE) was added, and samples were centrifuged for 1 minute at 8,000 rpm. Samples were removed from the centrifuge, microcentrifuge tubes with precipitate were saved, and the mini-spin columns were placed in new microcentrifuge tubes, 200 µl of elution buffer (Buffer AE) was added, and samples were again centrifuged for 1 minute at 8,000 rpm. Microcentrifuge tubes for each sample were combined, mini-spin columns were discarded, and samples were then stored at -80 $^{\circ}$C.

1.2.6.2 Microsatellites

Microsatellite primers were obtained from Dr. James Strange at the Pollinating Insect-Biology, Management and Systematics Research Unit of USDA-ARS at Utah State University, who had previously identified appropriate microsatellite primers that target *Bombus* spp. Microsatellite concentrations were obtained with specific amounts to be used with each DNA sample. 10 microsatellite primers were originally used to assess genetic diversity; however, two of 10 primers failed to amplify successfully; therefore, we used the remaining eight primers. Primers were split into two groups

(plexes) to prevent hybridization between primers that share overlapping size ranges. Each plex was prepared separately with corresponding primer amounts depending on the primer, and the amount of water was adjusted to total a 8 µl solution. Each mixture was then combined with 2 µl DNA from each sample and placed in a thermocycler. The thermocycler was first warmed up to 95 °C and then proceeded with the following cycles: Step 1: No repeats at 95 °C for 3:30; Step 2: 30 repeats at 95 °C for 0:30, 55 °C for 1:15, and 72 °C for 0:45; Step 3: No repeats at 72 °C for 15:00; Step 4: Hold at 15 °C for infinity. Samples were sent to Delaware Biotechnology Institute (DBI) to be sequenced. DBI forwarded data files back of the sample sequences, and each allele was scored using Genemapper version 3.7.

Once allele frequencies were scored, the samples were filtered to separate out male individuals (since they are all homozygous) and any samples that had fewer than four replicated loci. Samples were uploaded into Microchecker version 2.2.3 to test for and remove null alleles (van Oosterhout *et al.,* 2004).

1.2.7 Statistical analysis

R statistical software (*unmarked* package) was used to test the statistical significance of the collected data. We predicted bee abundance from site variables using multinomial *N*-mixture models using the function *gmultmix* for removal sampling in populations open to temporary migration with *N* having a negative binomial distribution. We modeled the effect of covariates on bee abundance and compared models based on Akaike's information criterion (AIC) (Burnham and Anderson 2002). To determine the relative importance of each covariate in predicting abundance, we calculated and summed the cumulative model weights (AICwt) (Burnham and Anderson 2002). We considered models with $\Delta AIC < 5.0$ to be

equivalent and calculated model-averaged parameter estimates among equivalent top-ranked models.

Table 1.2: Variables collected within and around each field site with corresponding mean and standard error.

Covariate	Abbreviation	Mean ±1 SE
Percent ag at 1000m	ag1000	0.13 ± 0.02
Percent impervious at 1000m	imperv1000	0.24 ± 0.01
Basal ft^2/acre (tree density)	basal	119.71 ± 5.69
Litter volume in liters	litter	5.18 ± 0.30
Nonnative stems per m^2	nnstems	10.80 ± 3.36
Native stems per m^2	nstems	7.96 ± 1.03
Nudds (understory density)	nudds	30.15 ± 2.16
Organic matter % mean	organic	10.26 ± 0.79
Patch size (ha)	patch	56.59 ± 6.82
pH	ph	4.90 ± 0.10

Table 1.3: Models used to predict abundance including their multivariate parameters.

Model	Variables
Landscape	imperv1000, ag1000, patch
Veg	nstems, nnstems, nudds, basal
Soil	organic, litter, ph
Global	imperv1000, ag1000, patch, nstems, nnstems, nudds, basal, organic, litter, ph
Null	None

To determine the factors that best predicted bee abundance, we modeled the effect of 10 covariates for each bee guild (Table 1.2). Point-specific covariates included tree density (measured with a prism), understory density (measured with Nudds boards), volume of leaf litter, soil pH, native stem mass, nonnative stem mass

and percent organic matter. Site-specific covariates included patch size in hectares, percent surrounding landscape as agriculture at 100, 250, 500, and 1000m, and percent surrounding landscape as impervious surface at 100, 250, 500, and 1000m. Percent agriculture at 100 and 500, and percent impervious surface at 100 and 500 were highly correlated ($r^2 > 0.8$), and literature suggested that 750 m distances impacted pollinators, therefore only one distance (1000 m) for both surrounding landscape covariates was analyzed for predicted bee abundance. Covariates were separated into three categories: Landscape (ag1000, imperv1000, patch), Soil (litter, ph, organic), and Vegetation (basal, nnstems, nstems, nudds), and each multivariate model consisted of the associated covariates. (See Table 1.2, 1.3). All models were then ranked by best to worst in predicting bee abundance. Lambda coefficients for each model then explained which variable within the specific model was strongly influencing model performance, with values deviating the furthest from 0 being the most influential variable.

Each covariate had a specific prediction regarding its impact on abundance. Tree density was predicted to positively correlate with bee abundance since more trees could indicate an older and more established forest fragment. Understory density was predicted to positively impact abundance because some bees nest in stems and more understory could indicate more floral resources on the understory plants. Leaf litter was predicted to positively impact bee abundance since more leaves could indicate an older and more established forest fragment with increased soil nutrition. Soil pH was predicted to either positively or negatively impact abundance since the effect of pH impacting ground nesting bees is not well studied. Native stem and nonnative stem mass were predicted to positively and negatively, respectively, predict abundance

since most native pollinators utilize native plants over nonnative plants. Percent organic matter was predicted to positively relate to abundance since higher organic matter could indicate more nutritious soil. Percent agriculture and percent impervious surface in surrounding landscape were predicted to negatively influence abundance due to lower floral diversity. Beta diversity indices using Bray-Curtis dissimilarity (Bray and Curtis, 1957) and within patch variation were calculated using R (*vegan*).

Microsatellite allele data was formatted for the program Genetix version 4.05 to visually observe population grouping via allele frequency data, and to convert data into additional input files for future programs. Samples were also uploaded into the Bayesian based population genetics software Structure version 2.3.4 to determine population structure and the true value of K or number of populations. The program Genepop (version 4.2) (Raymond and Rousset, 1995; Rousset 2008) was used to determine deviations from Hardy-Weinberg equilibrium, linkage disequilibrium, and to test for expected and observed heterozygosity. The program Structure Harvester vA.2 was used to verify the number of populations or K using the Evanno Method (Earl and vonHoldt 2012). FSTAT (version 2.9.3) was used to determine allelic richness per locus and population, and Fst values. The program HP-Rare 1.0 was used to compute the number of private alleles using rarefaction which adjusts the numbers of alleles within a population to account for differing sample sizes (Kalinowski, 2005).

1.3 Results

Three bowl traps were collected at five points throughout 14 sites for nine visits (n = 1,890) for each field season. The three different colored bowls were pooled into one bowl for analysis (n = 630). More bees were collected and higher species richness was detected in 2013 compared to 2014 (1,591 bees and 107 species versus

1,216 bees and 67 species, respectively) (Figure 1.5). In both field seasons, *Andrena erigeniae* Robertson was the most commonly caught species (n = 256 in 2013, n = 254 in 2014); *Lasioglossum subviridatum* was the second most commonly caught species in 2013 (n = 122), and in 2014 *Andrena carlini* was the second most commonly caught species while it was the 6th most commonly caught species in 2013 (n = 92 in 2013, n = 245 in 2014 respectively) (Table 1.4). Genus counts varied between years, with mostly fewer individuals in each genus in 2014 (Table 1.5). Sweep netted bee counts were compiled for both years and separated between interior sweeping (inside the site, Figure 1.4), edge sweeping (edge of site/forest fragment, Figure 1.5), and exterior sweeping (Figure 1.6). Interior bee samples consisted mostly of *Andrena, Nomada,* and *Lasioglossum* species (Figure 1.4). Edge bee samples consisted of a variety of genera including *Bombus*, *Ceratina, Andrena,* and *Nomada* (Figure 1.5). Exterior bee samples consisted mostly of *Bombus* and *Ceratina* bees (Figure 1.6). Bee community, therefore, differed depending on the forest location, where *Andrena* occurred more in and along the edge of forest patches, and *Bombus* occurred along the edge and outside of the forest.

Table 1.4: Species count, ordered by the 20 most numerous species of 2013. 2014 species count displayed, and change between years with reductions in red and additions in black.

Species	2013	2014	Change
Andrena erigeniae	256	254	-2
Lasioglossum subviridatum	125	130	5
Nomada luteoloides	107	27	-80
Ceratina calcarata	99	33	-66
Nomada depressa	97	1	-96
Andrena carlini	92	245	153
Osmia taurus	69	44	-25
Osmia pumila	62	55	-7
Andrena violae	49	81	32

Andrena nivalis	46	1	-45
Osmia cornifrons	38	8	-30
Lasioglossum gotham	35	43	8
Osmia georgica	31	4	-27
Andrena pruni	30	47	17
Nomada pygmaea	28	22	-6
Augochlora pura	26	13	-13
Nomada imbricata	24	3	-21
Andrena perplexa	23	8	-15
Ceratina strenua	20	6	-14
Nomada armatella	19	0	-19

Table 1.5: Genus count, 2013, 2014, and change between years with reductions in red and additions in black.

Genus	**2013**	**2014**	**Change**
Agapostemon	2	1	-1
Andrena	654	687	33
Apis	5	0	-5
Augochlora	26	13	-13
Augochlorella	1	0	-1
Augochloropsis	4	0	-4
Bombus	12	7	-5
Ceratina	126	44	-82
Colletes	2	0	-2
Halictus	19	7	-12
Hylaeus	1	0	-1
Lasioglossum	216	242	26
Nomada	309	99	-210
Osmia	212	112	-100
Sphecodes	6	3	-3
Total	1595	1215	-380

Table 1.6: Genus count at Christina Creek 2, 2013, 2014, and change between years with reductions in red and additions in black.

Genus	**2013**	**2014**	**Change**
Andrena	52	66	14
Augochlora	0	1	1
Augochloropsis	1	0	-1
Bombus	1	0	-1
Ceratina	42	13	-29
Halictus	1	0	-1
Lasioglossum	7	3	-4

Nomada	6	6	0
Osmia	20	13	-7
Total	130	102	-27

Table 1.7: Genus counts at Webb Farm, 2013, 2014, and change between years with reductions in red and additions in black.

Genus	2013	2014	Change
Andrena	82	83	1
Augochlora	1	0	-1
Bombus	1	0	-1
Ceratina	3	2	-1
Halictus	0	1	1
Lasioglossum	13	0	-13
Nomada	19	3	-16
Osmia	6	3	-3
Sphecodes	2	0	-2
Total	127	92	-35

Table 1.8: Genus counts at White Clay 1, 2013, 2014, and change between years with reductions in red and additions in black.

Genus	2013	2014	Change
Andrena	93	59	-34
Apis	1	0	-1
Augochlora	3	1	-2
Augochloropsis	1	0	-1
Bombus	1	0	-1
Ceratina	3	0	-3
Halictus	4	0	-4
Lasioglossum	19	14	-5
Nomada	66	13	-53
Osmia	32	6	-26
Total	223	93	-130

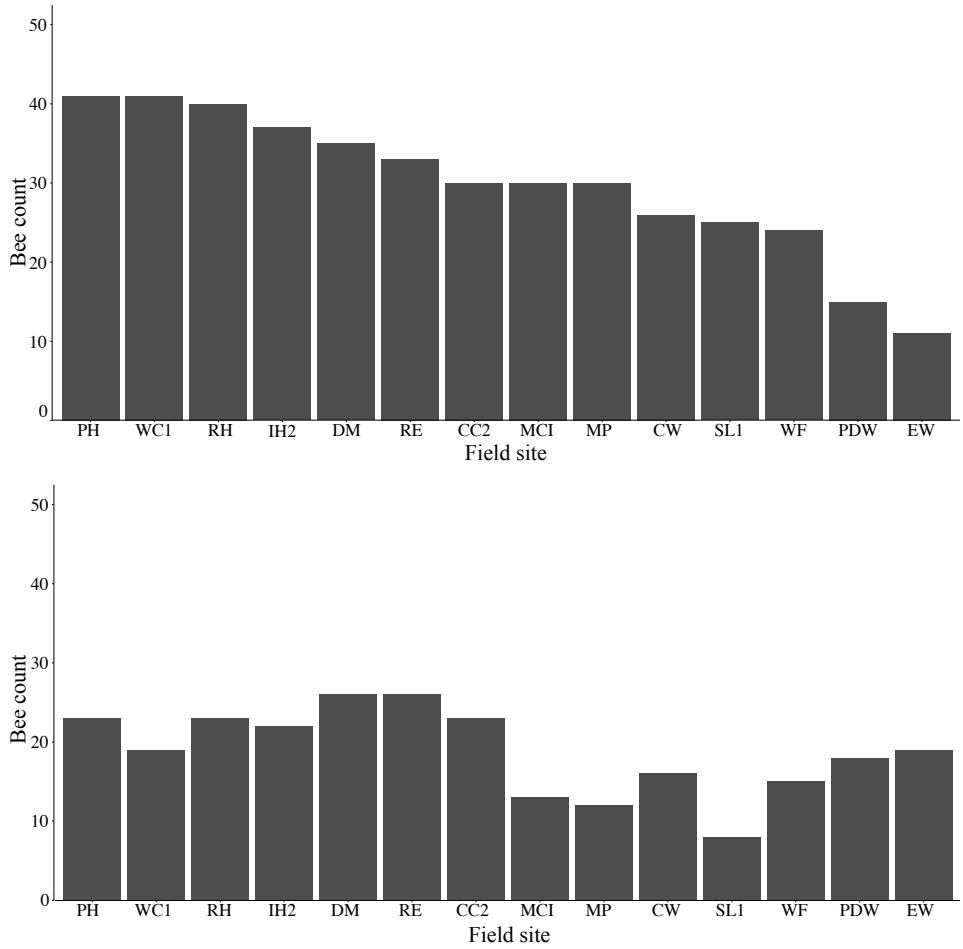


Figure 1.3: Species richness at each field site (see Table 1.1 for abbreviations), 2013 (top) and 2014 (bottom) respectively. Bee counts consisted of bees collected from only bowl traps.

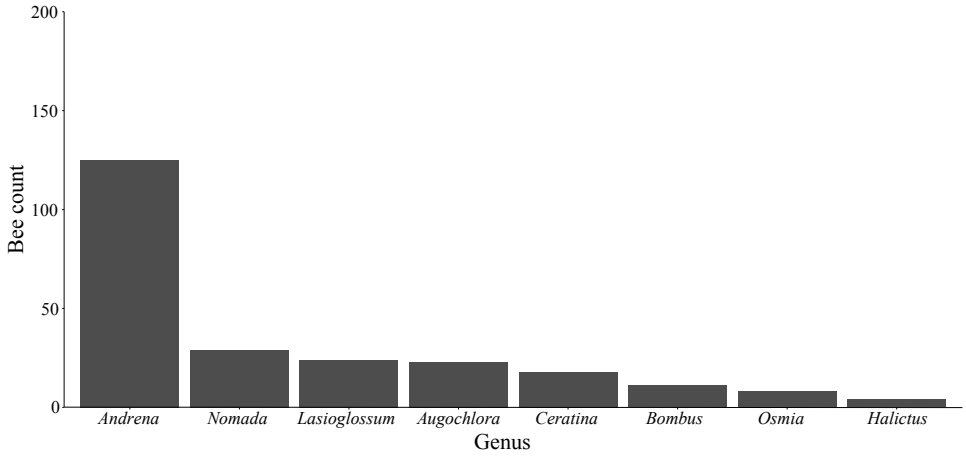


Figure 1.4: Interior bee catch in eight most numerous genera, 2013 and 2014 collectively. Bee counts consisted of bees collected from only sweep nets.

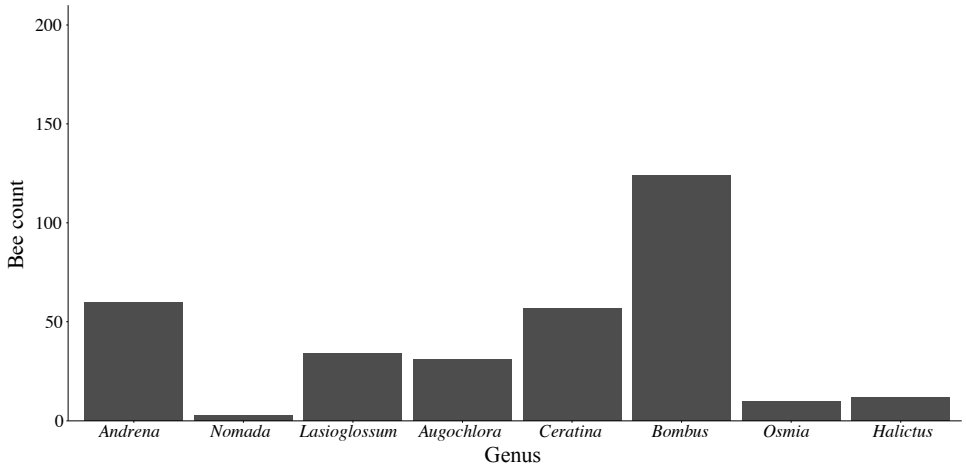


Figure 1.5: Edge bee catch in eight most numerous genera, 2013 and 2014 collectively. Bee counts consisted of bees collected from only sweep nets.

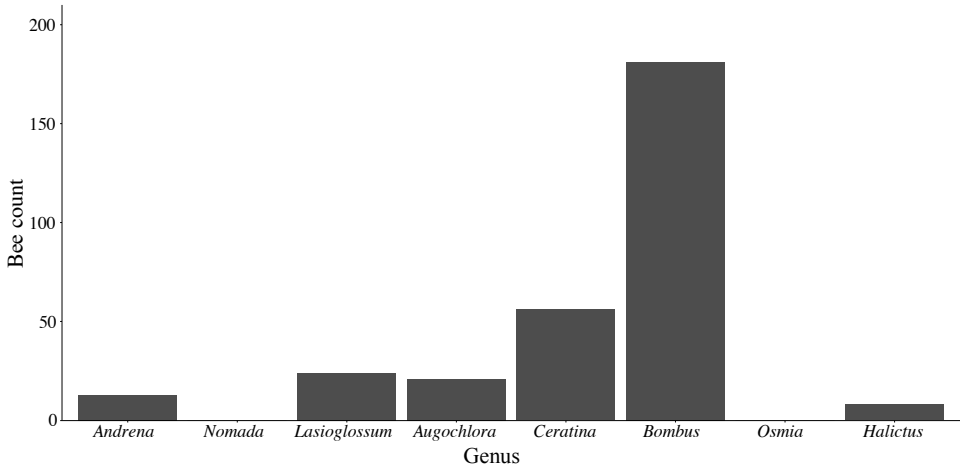


Figure 1.6: Exterior bee catch in eight most numerous genera, 2013 and 2014 collectively. Bee counts consisted of bees collected from only sweep nets.

1.3.1 Phenology

The phenology of collected bees differed between genera, family, and species over the two field seasons. In 2013 bees were present and more individuals were collected in bowl traps throughout April and May. In 2014 peak bee collection occurred in mid-late April (Figure 1.7), but overall bee counts were lower compared to 2013. This pattern is seen specifically in *Andrena* and *Lasioglossum* between both collecting years (Figure 1.8, Figure 1.10). Both field seasons yielded similar emergence times in early April; however, there appeared to be differences in peak visitation rates in April and May. There was a notable difference between the number of *Ceratina, Nomada,* and *Osmia* collected between years, with fewer individuals collected in 2014 (Figure 1.9, 1.11, 1.12) whereas *Lasioglossum* were collected in similar amounts both years (Figure 1.10). *Andrena erigeniae* was collected in larger numbers in 2013 compared to 2014, but each collection event in 2014 consisted of more individuals compared to 2013 (Figure 1.14). *Andrena carlini* phenology appears

to be limited to April and early May with substantially higher numbers in 2014 compared to 2013 (Figure 1.13). *Lasioglossum subviridatum* was collected between early April and late May with no obvious differences between years (Figure 1.15).

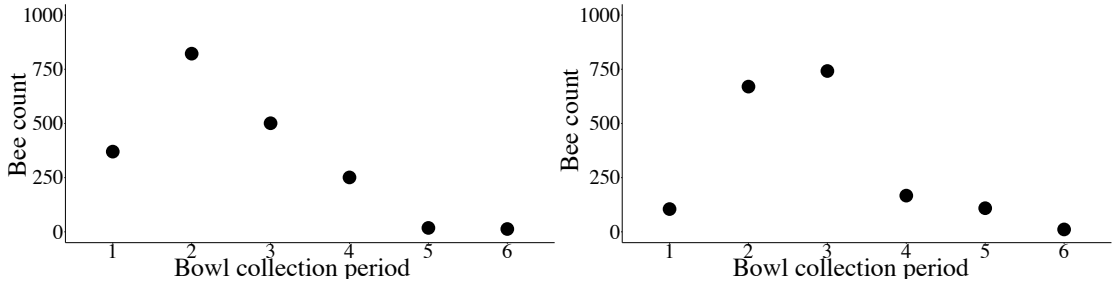


Figure 1.7: All bee phenology pooled by collection event, 2013 (left) and 2014 (right) respectively. Bee counts consisted of bees collected from only bowl traps.

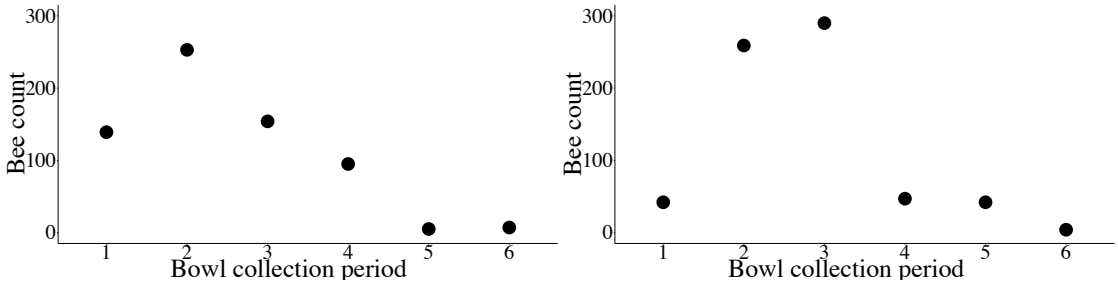


Figure 1.8: *Andrena* phenology pooled by collection event, (left) and 2014 (right) respectively. Bee counts consisted of bees collected from only bowl traps.

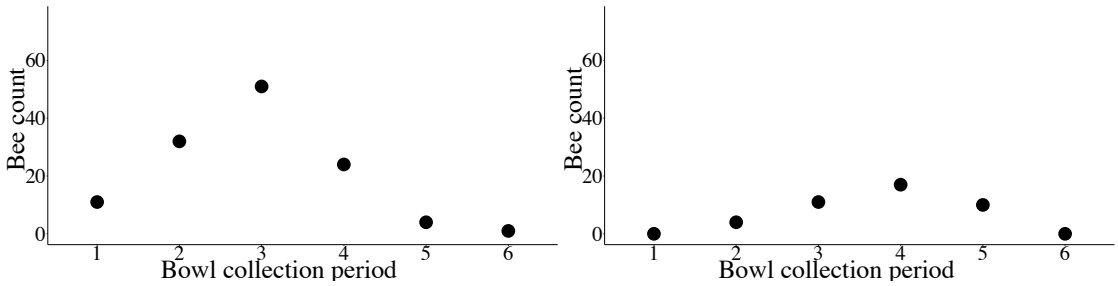


Figure 1.9: *Ceratina* phenology pooled by collection event, 2013 (left) and 2014 (right) respectively. Bee counts consisted of bees collected from only bowl traps.

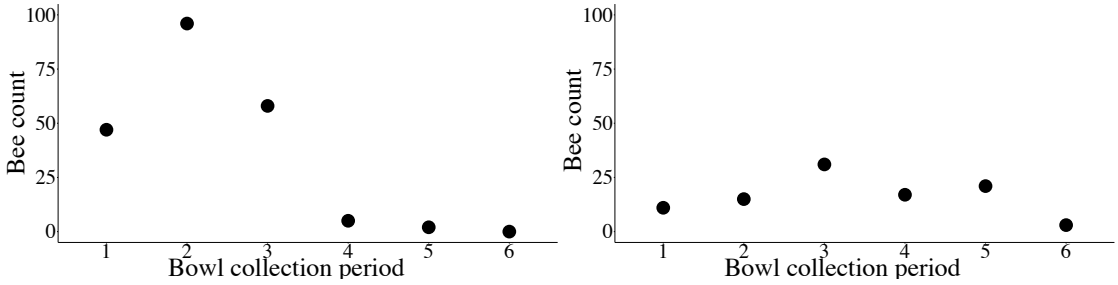


Figure 1.10: *Lasioglossum* phenology pooled by collection event, 2013 (left) and 2014 (right) respectively. Bee counts consisted of bees collected from only bowl traps.

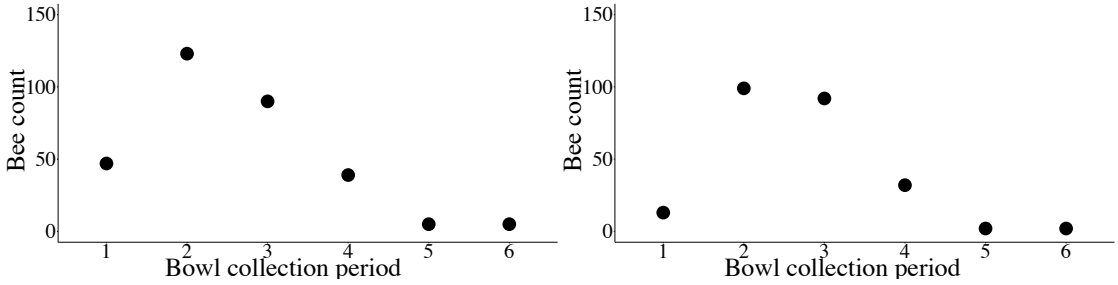


Figure 1.11: *Nomada* phenology pooled by collection event, 2013 (left) and 2014 (right) respectively. Bee counts consisted of bees collected from only bowl traps.

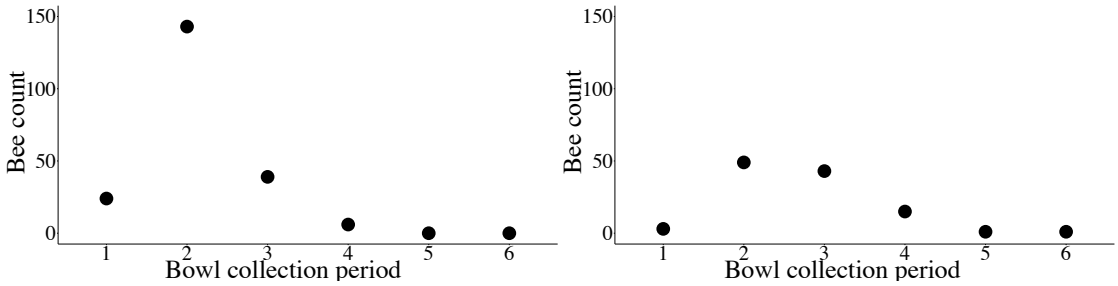


Figure 1.12: *Osmia* phenology pooled by collection event, 2013 (left) and 2014 (right) respectively. Bee counts consisted of bees collected from only bowl traps.

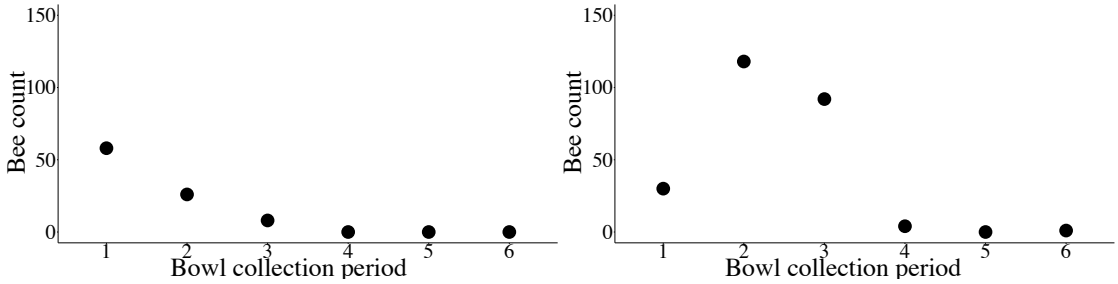


Figure 1.13: *Andrena carlini* phenology pooled by collection event, 2013 (left) and 2014 (right) respectively. Bee counts consisted of bees collected from only bowl traps.

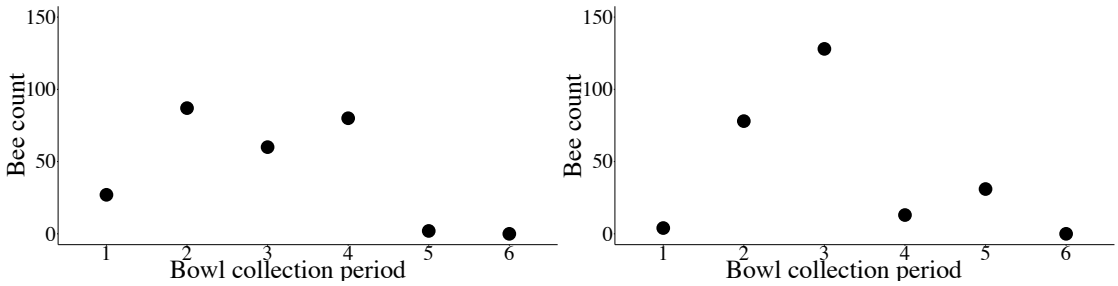


Figure 1.14: *Andrena erigeniae* phenology pooled by collection event, 2013 (left) and 2014 (right) respectively. Bee counts consisted of bees collected from only bowl traps.

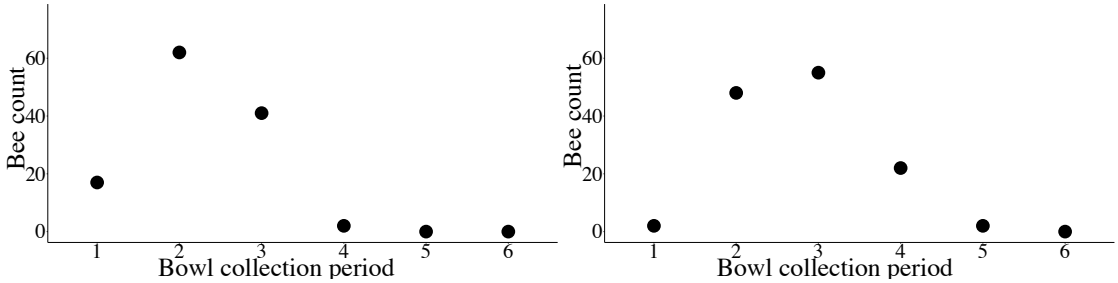


Figure 1.15: *Lasioglossum subviridatum* phenology pooled by collection event, 2013 (left) and 2014 (right) respectively. Bee counts consisted of bees collected from only bowl traps.

1.3.2 Beta diversity within sites

Beta diversity was calculated between each point within a site, then plotted and averaged for the entire site for both field seasons (Figure 1.16). Higher beta diversity indicates greater species diversity between two points. Christina Creek 2 showed the highest average beta diversity at each point where Iron Hill 2 showed the lowest average beta diversity at each point. Variations in beta diversity between points were highest at White Clay 1 and Mount Cuba Interior, and lowest at Peacedale West,

indicating that beta diversity between points was vastly different compared to one another within the same site.

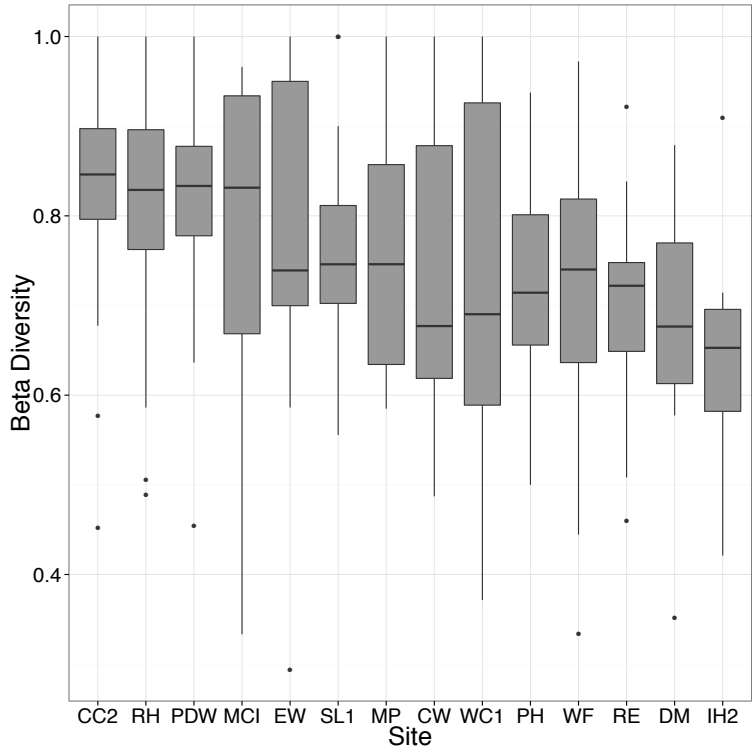


Figure 1.16: Beta diversity averaged for each site. Sites are ordered from highest mean beta diversity to lowest. Gray boxes indicate 1st and 3rd quartile; black horizontal lines indicate 2nd quartile. Dark vertical lines indicate 1.5*IQR (distance between 1st and 3rd quartiles) in both directions of 2nd quartile. Visible dots represent outliers.

1.3.3 Abundance modeling

Abundance modeling was calculated for the following groups of bees: Andrenidae, Halictidae, Megachilidae*, Nomada spp.* (both Apidae), *Ceratina spp.,* and *Andrena erigeniae*. Modeling was conducted by combining 2013 and 2014 collected data since bees naturally fluctuate each year and our goal was to examine abundance,

not annual fluctuation. Models that ranked higher than ΔAIC of 5 were considered for results.

1.3.3.1 *Andrena*

The highest-ranking *Andrena* abundance model was the landscape model, and the variable that was most influential was percent agriculture at 1000 m (Table 1.9), showing that as agriculture increased, abundance of *Andrena* decreased. The second highest-ranking model was the vegetation model, and the variable that was most influential was understory density, where *Andrena* abundance decreased with an increase in understory density.

Table 1.9: Multivariate models ranked from best predicting *Andrena* abundance to least using delta AIC values. Lambda coefficient values for each covariate are indicated under each variable column. Most extreme lambda values are the variables within the corresponding model that best influence model performance (in bold).

Model	Ag1000	Basal	Imperv1000	Litter	Nnstem	Nstem	Nudds	Organic	Patch	pH	AIC	ΔAIC
landscape	**-0.40**	NA	-0.20	NA	NA	NA	NA	NA	-0.12	NA	-13.39	0.00
veg	NA	-0.19	NA	NA	-0.01	0.14	**-0.28**	NA	NA	NA	-11.23	2.16
global	-0.23	-0.19	0.07	0.11	0.06	0.12	-0.29	0.14	0.06	0.05	-7.55	5.84
soil	NA	NA	NA	0.10	NA	NA	NA	0.08	NA	0.06	-6.72	6.67
null	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	97.21	110.61

1.3.3.2 *Andrena erigeniae*

The highest-ranking model predicting abundance of *A. erigeniae* was the landscape model, which contained ag1000, imperv1000, and patch size (Table 1.10), showing that as agriculture increased, *A. erigeniae* abundance decreased. The second highest-ranking model was the null model, suggesting that the landscape model best

predicts *A. erigeniae* abundance. These results are somewhat consistent with the abundance predictions of the genus *Andrena*, but *A. erigeniae* responded more sensitively to increasing agriculture compared to the genus.

Table 1.10: Multivariate models ranked from best predicting *Andrena erigeniae* abundance to least using delta AIC values. Lambda coefficient values for each covariate are indicated under each variable column. Most extreme lambda values are the variables within the corresponding model that best influence model performance (in bold).

Model	Ag1000	Basal	Imperv1000	Litter	Nnstem	Nstem	Nudds	Organic	Patch	pH	AIC	ΔAIC
landscape	**-0.91**	NA	-0.34	NA	NA	NA	NA	NA	-0.38	NA	606.07	0.00
null	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	611.02	4.95
global	-0.79	-0.41	-0.06	0.09	-0.14	0.08	-0.16	0.30	-0.17	0.04	613.50	7.43
veg	NA	-0.42	NA	NA	-0.09	0.11	-0.25	NA	NA	NA	614.01	7.94
soil	NA	NA	NA	0.04	NA	NA	NA	0.21	NA	0.23	615.86	9.79

1.3.3.3 *Ceratina*

Ceratina abundance was best predicted by the landscape model, which included ag1000, imperv1000, and patch size (Table 1.11). Within the landscape model, the covariate that best predicted *Ceratina* abundance was patch size and percent agriculture at 1000m, showing that as patch size and amount of agriculture increased, *Ceratina* abundance is predicted to decrease. The global model was the second-highest ranked model to predict abundance of *Ceratina,* indicating that other covariates that were not tested may efficiently predict abundance.

Table 1.11: Multivariate models ranked from best predicting *Ceratina* abundance to least using delta AIC values. Lambda coefficient values for each covariate are indicated under each variable column. Most extreme lambda values are the variables within the corresponding model that best influence model performance (in bold).

Model	Ag1000	Basal	Imperv1000	Litter	Nnstem	Nstem	Nudds	Organic	Patch	pH	AIC	ΔAIC
landscape	**-0.47**	NA	-0.45	NA	NA	NA	NA	NA	**-1.22**	NA	559.09	0.00
global	**-0.57**	0.00	-0.06	-0.15	0.41	-0.24	0.25	0.03	**-0.79**	-0.12	559.29	0.20
veg	NA	0.00	NA	NA	0.38	0.04	0.10	NA	NA	NA	569.84	10.75
soil	NA	NA	NA	-0.18	NA	NA	NA	0.02	NA	0.14	579.25	20.15
null	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	597.70	38.61

1.3.3.4 Halictidae

The highest-ranking model predicting Halictidae abundance was the vegetation model, and the covariate that best influenced that model was understory density (Nudds), where abundance decreased with increasing understory density (Table 1.12). The global model was the second-highest ranked model to predict abundance of Halictidae, indicating that other covariates that were not tested may efficiently predict abundance.

Table 1.12: Multivariate models ranked from best predicting Halictidae abundance to least using delta AIC values. Lambda coefficient values for each covariate are indicated under each variable column. Most extreme lambda values are the variables within the corresponding model that best influence model performance (in bold).

Model	Ag1000	Basal	Imperv1000	Litter	Nnstem	Nstem	Nudds	Organic	Patch	pH	AIC	ΔAIC
veg	NA	-0.26	NA	NA	0.10	0.09	**-0.54**	NA	NA	NA	804.17	0.00
global	-0.08	-0.19	-0.47	0.19	0.05	0.11	-0.46	-0.23	-0.42	-0.12	807.58	3.41
landscape	-0.31	NA	-0.55	NA	NA	NA	NA	NA	-0.37	NA	809.62	5.45
soil	NA	NA	NA	0.14	NA	NA	NA	-0.16	NA	-0.15	814.13	9.95
null	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	815.44	11.27

1.3.3.5 *Osmia*

The highest-ranking model to predict *Osmia* abundance was the global model, which included every covariate, suggesting that other variables not tested may predict *Osmia* abundance more accurately (Table 1.13). The variables that highly influenced the global model score were patch size and increasing impervious surface at 1000m, where *Osmia* abundance increased with an increase in impervious surface and patch size. The second-highest ranked model was the landscape model, which also included impervious surface and patch size as highly influential variables.

Table 1.13: Multivariate models ranked from best predicting *Osmia* abundance to least using delta AIC values. Lambda coefficient values for each covariate are indicated under each variable column. Most extreme lambda values are the variables within the corresponding model that best influence model performance (in bold).

Model	Ag1000	Basal	Imperv1000	Litter	Nnstem	Nstem	Nudds	Organic	Patch	pH	AIC	ΔAIC
global	0.03	-0.10	**0.74**	0.10	0.33	0.16	-0.13	-0.10	**0.93**	0.22	659.84	0.00
landscape	-0.13	NA	**0.25**	NA	NA	NA	NA	NA	**0.38**	NA	664.50	4.66
soil	NA	NA	NA	0.15	NA	NA	NA	-0.26	NA	0.10	665.71	5.87
null	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	667.39	7.56
veg	NA	-0.12	NA	NA	0.13	-0.02	-0.03	NA	NA	NA	669.94	10.11

1.3.3.6 *Nomada*

The highest-ranking model to predict *Nomada* abundance was the landscape model, which included ag1000, imperv1000, and patch. The variables that most influenced the landscape model were patch size and agriculture at 1000m, where *Nomada* abundance increased with an increase in patch size and decreased with an increase in agriculture surrounding the landscape (Table 1.14).

Table 1.14: Multivariate models ranked from best predicting *Nomada* abundance to least using delta AIC values. Lambda coefficient values for each covariate are indicated under each variable column. Most extreme lambda values are the variables within the corresponding model that best influence model performance (in bold).

Model	Ag1000	Basal	Imperv1000	Litter	Nnstem	Nstem	Nudds	Organic	Patch	pH	AIC	ΔAIC
landscape	**-0.41**	NA	0.07	NA	NA	NA	NA	NA	**0.45**	NA	811.91	0.00
global	-0.34	-0.03	0.13	0.08	0.13	0.05	-0.22	-0.02	0.48	-0.09	823.05	11.14
veg	NA	-0.19	NA	NA	-0.01	-0.06	-0.33	NA	NA	NA	825.62	13.72
soil	NA	NA	NA	0.18	NA	NA	NA	-0.27	NA	-0.17	826.21	14.30
null	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	844.98	33.07

1.3.4 Genetic analysis

All sweep netted samples of bumble bees were identified and separated by species. The two most common species caught, *Bombus bimaculatus* and *B. impatiens* were used for genetic analysis.

FCA plots showed genetic differentiation in *B. impatiens* and *B. bimaculatus* (Figure 1.17, 1.18). *B. impatiens* populations overlapped with the exception of bees collected from Reservoir, indicating that there was a high level of gene flow between sites. *B. bimaculatus* samples showed little genetic overlap with a marked distinction in bees collected from Webb Farm, indicating that bees from these sites were somehow isolated.

Structure barplots for both species showed how individuals and populations differentiated when given an estimated population size. *B. bimaculatus* showed both genetic and geographical differentiation when the estimated population (K) was at least 2 (Figure 1.19). Bees collected from Christina Creek 1, Ecology Woods,

Peacedale West, and half of the bees caught at White Clay 1 belong to one population and bees caught from Chrysler Woods, half of White Clay 1, and Webb Farm belong to another population, suggesting that there may be two populations of this species. *Bombus bimaculatus* bees collected from Webb Farm were shown to be genetically different using FCA analysis. When analyzed using the program Structure, bees from Webb Farm were seen to belong to a separate population, further suggesting that two populations exist. Structure HARVESTER estimated population size using ΔK and these results agreed with the assumption of *B. bimaculatus* having a population size of 2 (Figure 1.20). The Structure barplot of *B. impatiens* showed no genetic or geographic differentiation depending on the estimated population size, and Structure HARVESTER indicated that there might be six populations. These conflicting results suggest that there is not enough information to accurately estimate the true population size of *B. impatiens* occurring in the fragments.

Since both species had low sample sizes, we looked at private or unique alleles after rarefaction using HP-RARE and expected and observed heterozygosity using Genepop. *Bombus impatiens* individuals had the lowest number of private alleles from Peacedale and the highest number of private alleles and highest expected heterozygosity from Reservoir (Table 1.15), which further supports that *B. impatiens* collected from Reservoir are genetically distinct from other locations. *Bombus bimaculatus* individuals had the lowest number of private alleles from Christina Creek 2 and the highest from White Clay 1 (Table 1.16). White Clay 1, according to the Structure barplot (Figure 1.27), is split between two potential populations and also has the highest number of private alleles. Individuals from Chrysler Woods, White Clay 1, and Webb Farm had the three highest private alleles and high expected and observed

heterozygosity, which further supports the notion that these bees form a separate and distinct population.

In *B. bimaculatus*, locus BL13 from White Clay 1, BTMS62 from Webb Farm, and BTMS86 from White Clay 1 were the only loci not in Hardy-Weinberg Equilibrium, and in *B. impatiens*, all loci were in Hardy-Weinberg Equilibrium. In terms of heterozygosity deficiency, *B. bimaculatus* was deficient at White Clay 1 and Webb Farm, and at BL13, BTMS62, and BTMS86. *Bombus impatiens* was deficient at Ecology Woods and Peacedale West, and at BL13 and BTMS62. Neither species showed signs of linkage disequilibrium.

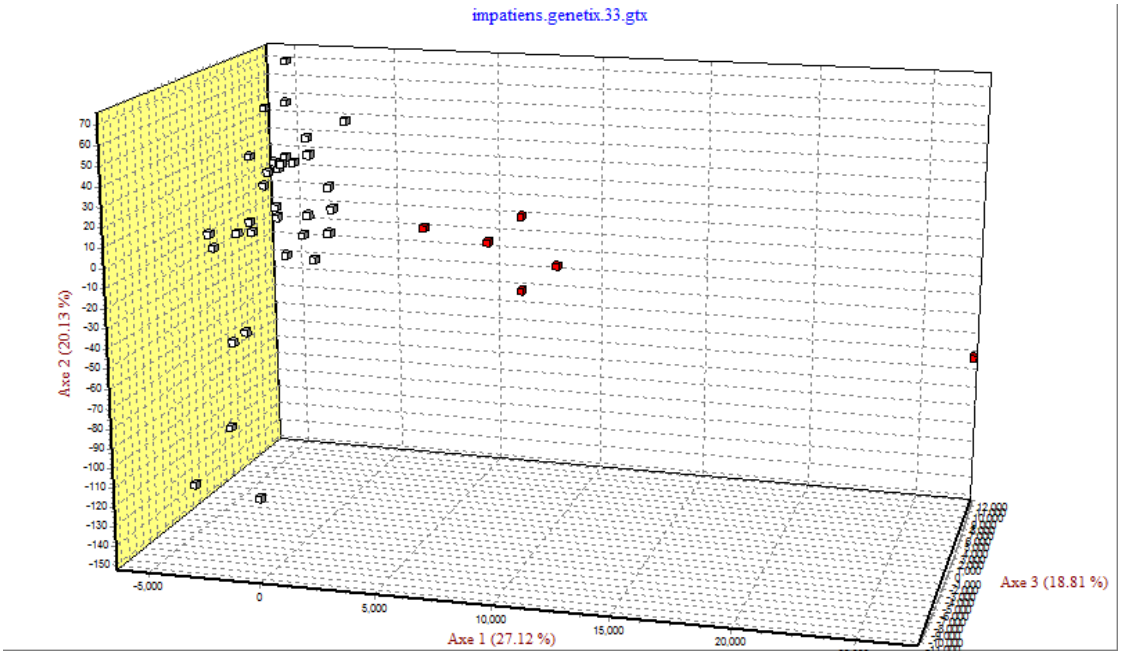


Figure 1.17: Visual representation of population structure in *B. impatiens.* White squares represent bees sampled from EW, PDW, PH, RH, SL1, and WC1. Red squares represent bees sampled from RE.

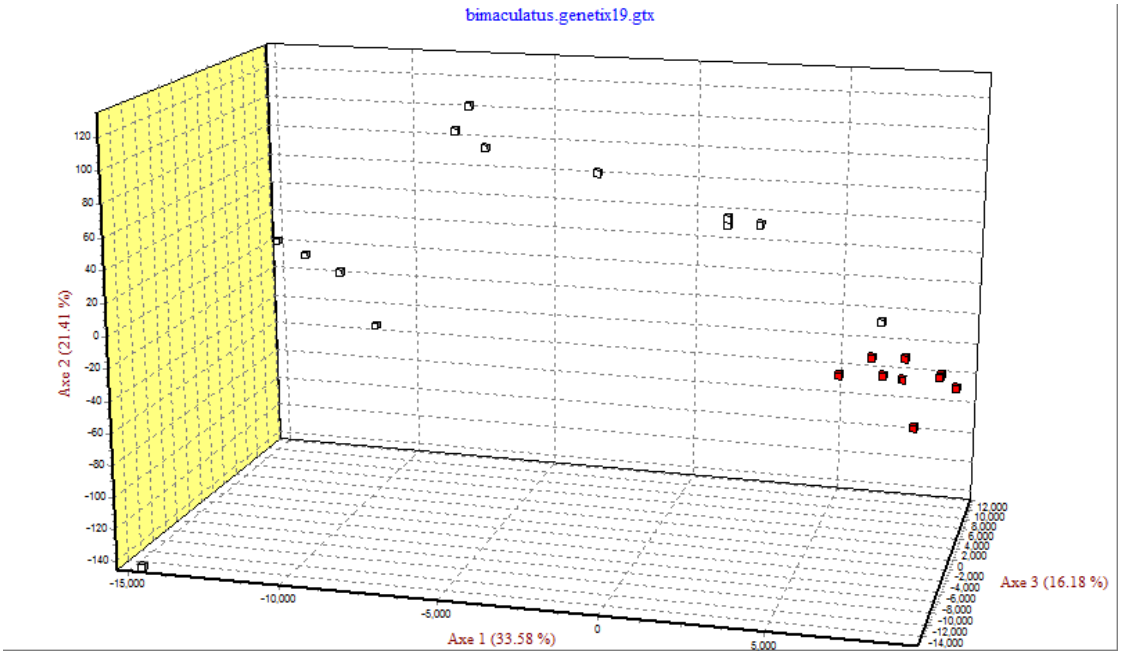


Figure 1.18: Visual representation of population structure in *B. bimaculatus.* White squares represent bees sampled from CC2, CW, EW, PDW, and WC1. Red squares represent bees sampled from Webb Farm.

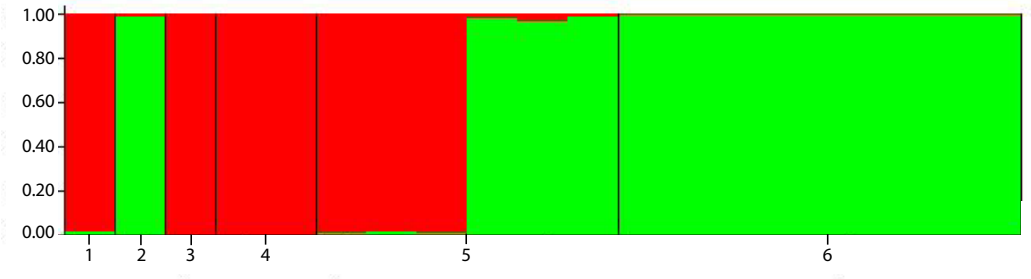


Figure 1.19: Structure barplot of *B. bimaculatus* when population number was set to 2. Each bar displays genetic information from each bee collected from the following sites: 1: CC2 (n=1), 2: CW (n=1), 3: EW (n=1), 4: PDW (n=2), 5: WC1 (n=6), 6: WF (n=7)(See Table 1.1 for abbreviations).

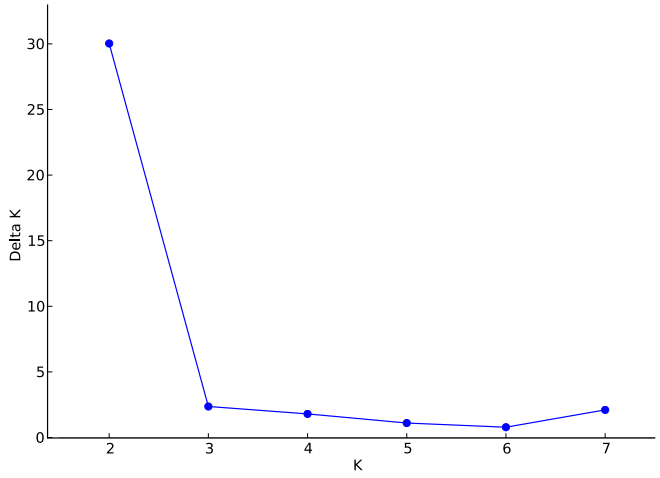


Figure 1.20: ΔK estimating the number of populations for *B. bimaculatus*. (ΔK: mean(|L(K)|)/sd(L(K)))

Table 1.15: Average allelic and private allelic richness after rarefaction for *Bombus impatiens* collected via sweep netting from seven forest fragments located in northern Delaware and southeastern Pennsylvania (See Table 1.1 for site abbreviations). Expected (H_E) and observed (H_O) heterozygosity are averaged between all loci for each site.

Site	Average allelic richness	Private allelic richness	H_E	H_O
EW	1.6	0.5	1.969	1.5
PWD	1.6	0.3	2.225	1.75
PH	1.6	0.4	2.256	2
RE	1.8	0.7	4.199	3.75
RH	1.5	0.3	1.575	1.5
SL1	1.6	0.4	1.925	1.75
WC1	1.7	0.5	3.819	3.875

Table 1.16: Average allelic and private allelic richness after rarefaction for *Bombus bimaculatus* collected via sweep netting from six forest fragments located in northern Delaware and southeastern Pennsylvania (See Table 1.1 for site abbreviations). Expected (H_E) and observed (H_O) heterozygosity are averaged between all loci for each site.

Site	Average allelic richness	Private allelic richness	H_E	H_O
CC2	1.3	0.3	NA	NA
CW	1.6	0.7	NA	NA
EW	1.1	0.4	NA	NA
PDW	1.4	0.5	0.905	0.857
WC1	1.8	0.8	4.057	2.875
WF	1.7	0.8	4.391	3.5

1.3.5 Pesticide analysis

Bees from six sites (White Clay 1, Chrysler Woods, Peacedale West, Philips, and Motorpool) were tested for pesticide exposure of over 200 compounds. Seventeen pesticides were found throughout the six sites, with the majority and typically highest levels found on bees sampled from White Clay 1 (Table 1.17). DDT was found on bees from Philips and Motorpool, and a DDT metabolite, DDE, was found on bees from all six sites. Imidacloprid was found on bees from all six sites at levels close to half of the recorded LD_{50} for honey bees (except at Chrysler Woods). Flucythrinate I and II were found only on bees from White Clay 1 and were near or above half of the recorded LD_{50} level for honey bees.

Table 1.17: List of pesticides detected in 3.5g bee samples collected from six FRAME sites (See Table 1.1 for abbreviations). Bee samples included individuals from the genera *Andrena, Bombus, Ceratina, Lasioglossum, Megachile, Nomada,* and *Osmia.* LD_{50} = dosage of chemical that kills 50% of honey bees, displayed in parts per billion (ppb); N/A = Not Available, ND = Not Detected, MLOQ = Method Limit Of Quantification,2 = Mullin et al 2010). All LD_{50} levels were cited from University of Hertfordshire's Pesticide Properties DataBase (http://sitem.herts.ac.uk/aeru/ppdb/en/index.htm).

Pesticide	LD_{50}	WC1	CW	PDW	PH	MP	MLOQ
4,4'-DDE	N/A	24.2	12.4	12.3	17.3	2.62	0.9
4,4'-DDT	*500*	ND	ND	ND	0.99	0.42	0.4
Acetamiprid	*809*	1.1	0.97	<MLOQ	<MLOQ	1.12	1
alpha-hexachlorohexane	N/A	10.7	6.7	4.1	8.7	3.9	0.5
Atrazine	*98,000*	<MLOQ	0.44	ND	ND	1	0.2
Bifenthrin	*10*	1.1	ND	ND	0.8	ND	0.5
Chloropyrifos	1,140[2]	2.22	1.84	2.9	<MLOQ	<MLOQ	0.8
Chlorothalonil	*4,000*	31	15.2	9	12.7	15.5	1
Cypermethrin	*20*	0.9	ND	ND	ND	ND	1
Dieldrin	*32*	2.05	ND	ND	<MLOQ	ND	1.1
Dimethomorph	*3,240*	2.5	ND	0.9	1	ND	1
Fenpropathrin	*5*	1.5	ND	ND	0.8	ND	1.3
Flucythrinate I	*7.8*	3.35	ND	ND	ND	ND	1.1
Flucythrinate II	*7.8*	4.34	ND	ND	ND	ND	1.1
Imidacloprid	*28*	9.44	<MLOQ	11.12	9.21	10.34	1.3
Methoxychlor	*2,360*	ND	<MLOQ	ND	ND	ND	0.6
Propanil	*9,430*	0.8	ND	0.7	<MLOQ	ND	0.6
Thiacloprid	*25,200*	1.51	<MLOQ	1.42	0.7	0.99	0.6

1.4 Discussion

Native pollinator abundance, diversity, and health are influenced by multiple factors that drive biodiversity throughout urban forest fragments. This study demonstrates the importance of forest fragments as suitable habitat for native pollinators and further reveals that native pollinators utilize mosaic and patchy landscapes for food and favorable nesting substrates. This study also reveals temporal

variation in native pollinator abundance and phenology within forested habitats, which is most likely in response to abiotic factors.

1.4.1 Species assemblage, richness, and phenology

1.4.1.1 Assemblage

Both field seasons yielded large numbers of bees, with 2013 yielding both more bees and species compared to 2014 (1,591 bees and 107 species versus 1,216 bees and 67 species, respectively) (Table 1.5). Fewer species in 2014 compared to 2013 may be a result of a harsher and longer winter between field seasons where entire species may have emerged in lower numbers and could have gone undetected. Resources may have also played a role directly, where low floral availability in 2013 could impact fewer offspring in 2014. *Nomada* populations were much lower in 2014 compared to 2013, and since these bees are parasites, they may have an oscillating emergence pattern that follows their host population emergence patterns. If there were fewer host individuals in 2013, then that could impact the 2014 *Nomada* population. *Nomada* have been seen to parasitize *Andrena*, but little is known about which *Nomada* species are parasites of which *Andrena* species. *Andrena carlini* had the largest change in species numbers between years with significantly more individuals in 2014. Variations in *A. carlini* counts between years may be a result of inadequate provisioning or high parasitism rates during 2012, which would impact the 2013 individuals, then the population may have rebounded during 2013 leading to an increase of individuals during 2014. This cascading effect may be species specific due to native pollinators being specialists, thus explaining why certain species appeared in high numbers one year and low numbers in a different year. Alternatively, different bee species may have stochastic

fluctuations in populations between years, which if only studied for two years may not be detected; therefore, continually monitoring bee populations is necessary to understand what variables are truly impacting their populations. A harsh winter, an increase in parasitism rates, or stochastic population fluctuations may be responsible for differences in the number of bees caught between years.

The bee community collected via sweep-netting varied depending on the location (Figures 1.4, 1.5, 1.6). Interior bee catch consisted mostly of *Andrena* species, while edge and exterior bee catch consisted mostly of *Bombus* spp., indicating that *Andrena* species are using the interior of the forest for food resources and nesting locations more than other locations. This is further supported by the decrease in *Andrena* species counts as we moved from the interior forest to edge and exterior sweeping locations. Similar findings were found in Brosi (2008), where bee community composition shifted between forests and pastures; tree-nesting bees were more abundant in larger, more contiguous forest patches and non-native *Apis* species were found in smaller, more disturbed patches. According to Fortel and colleagues. (2014), community structure, specifically parasitic species, increased as the percent of impervious surface reached an intermediate proportion. *Bombus* species were more common along the edge and exterior of forest patches compared to the interior. Bees caught along the edge and in the exterior represented more genera than bees collected in the interior of the forest fragments (20 genera vs. 11). This is most likely due to edge and exterior regions of forest fragments having a higher diversity of flowering plants throughout the season due to more consistent light conditions, and more nesting substrate availability, whereas the interior of the forest typically has few specific flowering plants. Certain bees such as *Bombus* species forage long distances and

respond positively to floral resources (Jha *et al.,* 2013), which may explain why bumble bees had higher visitation rates on the edge and exterior of forest patches.

Bowl samples were primarily collected between March and May whereas sweep netting occurred throughout the summer. Any *Bombus* spp. collected in bowl traps were typically queens, possibly searching for suitable nesting areas to establish colonies, instead of workers foraging for pollen and nectar in the more florally diverse edge and exterior locations.

Fluctuations in pollinator community structure, as seen in just two sampling years, suggest that interactions between pollinators and associated plant communities may be driven by opportunistic situations. Seeing that some but not all species were collected in varying densities between years also indicates that there other factors affecting the emergence and presence of species within these communities in advantageous or disadvantageous ways such as flowering time, disease, and ambient temperature just to name a few. An example of the complex interactions that may be impacting species abundance and richness in these fragments can be seen in *Nomada.* Many *Nomada* species are cleptoparasites on *Andrena* species and other ground nesting bees; therefore, their densities are reliant on the presence of their hosts. Since most cleptoparasites are specialists, a decrease in their host species would have negative impacts on their populations. The decline in *Nomada* in 2014 could have been the result of low host availability from the previous year, and this in turn could impact subsequent host populations. Fluctuations in bee species could be attributed to a lack of nutrition from the previous year, which could result in lower offspring numbers or underdeveloped offspring in subsequent years. A decrease in individuals, species, and pollinator community diversity in 2014 could simply indicate that 2013

was an unusually productive year for native bee communities compared to 2014, and that 2014 was a more "typical" year for bee populations. The causes behind the differences in bee abundance and richness in 2013 and 2014 are difficult to determine with only two field seasons worth of data. Having a longer-term data set would allow us to understand the mechanisms influencing native bee community diversity and abundance.

1.4.1.2 Richness

Species richness within each site varied between field seasons but remained similar when comparing the same site between field seasons, i.e., sites that had high species richness in 2013 typically had high species richness in 2014, and vice versa. Correlations between species richness and site characteristics revealed no significant correlation between characteristics and species richness. These results suggest that relationships between native pollinator richness and site characteristics are not straightforward and most likely occur at a more local level (flowers at a specific point) and not at the site level. These results agree with previous literature that found no differences in species richness in Douglas-fir forests compared to urban residential fragments (Wray *et al.,* 2014). Brosi and colleagues (2008) found that non-*Apis* Apidae (such as Meilponinae and Euglossinae bees) inhabited different forest types compared to *Apis*. We expected to see an increase in species richness and the number of bees with increasing patch size (e.g., Aizen and Fensinger 1994); however, we saw no significant correlation between species richness and patch size. This discrepancy may be due to the more forested sites lacking suitable and stable pan trap placement locations and instead were commonly vandalized or missing. Additionally, Cane and Sipes (2006) used patches ranging from 0.02ha – 5ha and Brosi *et al.,* (2008) surveyed

patch sizes that ranged from 0.25-250ha. Since we surveyed patches ranging from 2-163ha with a mean near 50ha (due to being in larger, contiguous forests), our narrow patch size range may be limiting species richness detections.

Bee richness has been positively associated with an increase in proximity to forest patches in cropping systems (Ricketts, 2004; Watson *et al.,* 2011; Bailey *et al.,* 2014), and near natural areas versus human dominated landscapes (Ramos and Santos, 2006). We found no correlation between bee richness and surrounding landscape (percent agriculture and percent impervious surface). Research has shown that forest fragments can act as refuges for native bees by providing both ample nesting substrates and early spring floral resources for native pollinators, while developed land may only provide limited floral resources in terms of type and phenology of bloom. The floral resources found in developed landscapes may not provide adequate nutrition for native pollinators due to the dominance of non-native, ornamental plants. Bee richness was high in all forest fragments regardless of the type of surrounding landscape, further supporting the idea that forest fragments can act as refuges for native pollinators.

Differences in bee abundance and species richness between field seasons suggest that several factors may be influencing bee richness. Anecdotally, in the winter of 2013-2014 many early-blooming plants had a delayed flowering time (possibly due to delayed growing degree-days), which may have affected the pollinators that utilized those plants. Pollinator communities also fluctuated between years, suggesting that certain species (e.g., *Andrena carlini*) might be more influenced by weather, disease, and floral resources than others. Bee densities in late April and early May were higher and lasted a shorter duration in 2014 compared to 2013. Since the bee community

between years varied, it is difficult to suggest what variables and to what degree they could be impacting native pollinators. *Andrena carlini* is noted to respond poorly to changes in forest loss and edge effects, but other pollinators may also be sensitive to these changes, which could impact how site characteristics correlate with species richness.

1.4.1.3 Phenology

Bee phenology was interpreted to understand the timing of emergence of pollinators in forest fragments and to determine how long bees were visiting bowl traps. The timing of bee emergence appeared to be consistent for both years, where bees were observed in bowl traps during the first week of April each season (Figure 1.7). Emergence time was also consistent between all bee genera. Bee collection peaked in late April/early May, and diminished at the beginning of June. In 2014 bee emergence had a similar trend but bee collection peaked higher and in a narrower time frame during mid-late April with few individuals caught in May.

Different emergence times and durations suggest that pollinators are highly synched with the availability of floral resources. Many of these bees emerged in early April when early blooming trees, shrubs, and spring ephemeral flowers were blooming. Bee phenology decreased near late May, which synchs with full leaf-out in forest fragments, thus reducing available forage in interior forest patches. Many studies looking at species richness of pollinators in both urban and forest settings do not address phenological differences between genera or variations between years. Phenological differences may be an important topic to explore in order to assess how weather variations impacts pollinators.

Differences in bee abundance and richness across years could be associated with a multitude of variables. Higher observance of different species, particularly *Andrena carlini*, may be associated with this species being more adapted to colder climates and harsher winters as these bees are found as far north as Alberta (Schrader *et al.,* 1978). The presence of high numbers of *Andrena erigeniae* in both years is likely due to an abundance of *Claytonia virginica*, their preferred flower for pollen, nectar, and mating locations, in all field sites (Barrows *et al.,* 1978). Due to the harsh winter between 2013 and 2014, flowering plants were delayed roughly two weeks; however, bee emergence occurred at the same time regardless of delayed flower development. This asynchrony could have negative effects on future bee populations, especially for specialist pollinators that are tied to the floral resources of a particular flower. Literature suggests that bee phenology is closely synched with flower phenology (Giles and Ascher 2006; Watson et al, 2011); therefore, flower timing and emergence may efficiently predict bee emergence.

1.4.2 Floral resources

Floral resources may be a key factor driving native bee diversity. This project saw an increase in bee genera in edge and exterior sections of forest fragments, and these locations typically have high densities of floral resources for extended periods throughout the summer. Interior forests, on the other hand, have fewer floral resources for a shorter period of time early in the spring. The discrepancy of more diverse native bees associated with disturbed habitats often overrides the importance of interior forest habitat for more specialized pollinators such as *Andrena erigeniae*. Bee presence is closely tied to flowering densities and timing. Spring ephemeral flowers blooming early to mid-April are critical nutritional resources for pollinators that emerge in the

early spring. Bees were observed visiting a wide variety of flowers (Table 1.20) regardless of whether the plant was native or non-native. This interaction between wild bees and non-native flowers may be beneficial for insects when their preferred floral resource is unavailable, but the nutritional resources from non-native flowers may hinder brood development. The variables collected through the FRAME project are beneficial for many forest-related projects; however, measuring floral emergence, density, and richness will be imperative to further predict pollinator abundance in these ecosystems.

1.4.3 Beta diversity

Many native pollinators are pollen specialists; therefore, uniqueness is even more important for this particular guild and for overall ecosystem function within a fragmented landscape. Unique or rare pollinators are especially susceptible to habitat loss; therefore, their relationship with plants is just as fragile. Beta diversity is used to describe the species uniqueness between locations to further interpret the importance of rare or unique individuals and where they occur in a landscape. The bee community sampled at Christina Creek 2 was the most unique and diverse, while the bee community sampled from Iron Hill 2 was the least unique and diverse (Figure 1.16). Correlations between beta diversity and site characteristics used to predict abundance were not statistically significant. Uniqueness throughout and between sites signifies that there are varying resources at the site and local level (point level, 25-50m) that attract native pollinators. These site and local landscape cues; however, may be different from the site characteristics that we used to analyze beta diversity correlations. Floral diversity, quantity and quality and nesting habitat quantity and

quality are variables that will need to be measured and correlated with beta diversity in future studies.

A significant portion of literature suggests that native pollinators decrease in richness and diversity with an increase in forest (Winfree *et al.,* 2007; Carper *et al.,* 2014); however, these studies sampled bees throughout the summer, well into when the forest canopy closes and sunlight is limited. During the summer, floral resources within forest patches are limited to disturbed areas and tree fall gaps where sunlight penetrates the forest floor, which is uncommon and patchy. Additionally, many studies suggesting that forests are poor bee sources have study sites dominated by evergreen and pine trees, which lack suitable floral resources for native bees. Data from this research supports studies (Taki *et al.,* 2007, Watson *et al.,* 2011) that emphasize the importance of deciduous forests as food resources for early spring pollinators that utilize spring ephemeral flowers. Early flowering trees such as Red Maple, Willow, Redbud, Black Locust and American Beech dominate urban and suburban forests in the Mid-Atlantic, and are crucial food resources for native and managed bees.

1.4.4 Abundance modeling

Native pollinators were divided into eight groups for abundance analysis (*Andrena* species, *Andrena erigeniae, Ceratina* species., *Nomada* species., Halictidae, and *Osmia* species). In previous studies, wild bee abundance was negatively correlated with the proportion of impervious surface and community structure also changed as a function of the proportion of impervious surface, with more parasitic bees in sites with an intermediate proportion of impervious surface (Fortel *et al.,* 2014).

In our study, bee abundance, with the exception of Halictidae and *Osmia,* was negatively impacted by an increase in forest fragmentation, in particular with an

increase in agriculture around the forest patch. Forest fragmentation according to this study's standards is defined as a patch of forest that has a varying surrounding landscape that does not solely consist of contiguous forests. Many studies investigating bee abundance in forest fragments define a fragment as an entity much more isolated than our fragments, with sizes ranging from 0.002 ha – 5ha (Cane and Sipes, 2006), where our study had fragment sizes ranging from 2ha to 163ha. If our sites had more drastic patch sizes as in other studies (the average patch size was over 50ha), we may have found stronger relationships between abundance and forest fragmentation. Overall, many studies focused on forest edges as opposed to interior forest bee abundance. Forest edges act as a reservoir for *Nomada* and *Andrena spp.* in agriculture ecosystems (Bailey *et al.,* 2014), which can benefit crop pollination, increase crop yield, and improve overall ecosystem services in edge habitats. Forest loss causes negative impacts on pollinator communities and seed sets of forest herbs, and abundance and species richness of bowl-collected bees was positively related to forest cover at a 750m radius (Taki *et al* 2007), and similarly, we found that agriculture surrounding forest patches at 1000m had negative impacts on bee abundance. Similar studies noted that the frequency of native bee visitation decreased with decreasing forest fragment size (Aizen and Fensinger, 1994), however we only found the opposite relationship between fragment size and bee abundance in *Ceratina*. For future studies, it is important to understand habitat diversity (Steffan-Dewenter *et al.,* 2002) in terms of floral resources, nesting substrates, and plant community structure for pollinators (Zurbuchen *et al.,* 2010) in order to predict abundance of all types of bees. Overall, minimal relationships were seen between impervious surface and bee abundance. These findings also support the notion that native pollinators are a

diverse and dynamic group of insects, which rely on many different site characteristics that may or may not have been tested

1.4.4.1 *Andrena*

The covariate that best predicted *Andrena* abundance was agriculture surrounding the site at 1000m (Table 1.9). As the percent of agriculture increased, *Andrena* abundance decreased. The multivariate model for landscape (ag1000, imperv1000, and patch size) ranked highest in predicting abundance. *Andrena* dominate the forest floor in early spring where their floral resources are located; therefore, it is logical for these bees to be negatively impacted by landscape that is not forest. The second highest-ranking model was the vegetation model, with the variable measuring understory density driving that model. High understory density may indicate that the forest fragment is an early successional fragment with a lack of canopy trees and high invasion rate of nonnative plants. *Andrena* are important pollinators of spring ephemeral flowers that are found in later successional forests and may not be as abundant in early successional forests. Sites with high understory density may also make navigating to flowers and proper nesting substrates challenging by changing the soil requirements needed for nesting, thus negatively impacting *Andrena* abundance.

1.4.4.2 *Andrena erigeniae*

Andrena erigeniae abundance was best predicted by the percent of agriculture surrounding the site, where abundance decreased with increasing agriculture (Table 1.10). The multivariate model for landscape (ag1000.mod, imperv1000.mod, patch.mod) highly predicted abundance, and the second highest singular model to

predict abundance was patch size, where abundance decreased with an increase in patch size. *A. erigeniae* is in the genus *Andrena* and was the most common bee collected, so this species and the genus should have similar abundance predictions. *Andrena* abundance was highly predicted by understory density, however *Andrena erigeniae* abundance was not, indicating that some species within a genus behave differently. Interestingly, *A. erigeniae* abundance decreased more dramatically with increasing agriculture and increasing patch size compared to the entire genus, suggesting that the species is more sensitive to these variables than the genus, and that *A. erigeniae* may thrive in smaller, more invaded forest fragments compared to the genus as a whole. *Andrena erigeniae* are specialists on *Claytonia virginica*, a common spring ephemeral flower that can dominate forest floors during early spring. Increasing agriculture and increasing tree density may have a negative impact on *Claytonia virginica*, which would in turn decrease *A. erigeniae* abundance. A survey of flower density may be a vital characteristic to predict abundance of *Andrena erigeniae*.

1.4.4.3 *Ceratina*

The highest-ranking model to predict *Ceratina* abundance was the landscape model (ag1000.mod, imperv1000.mod, patch.mod), and the second highest model was the global model, which included every covariate (Table 1.11). The highest singular covariate model to predict abundance was patch size, showing that as patch size increased, *Ceratina* abundance decreased (Figure 1.19). Agriculture was the second highest singular covariate to predict abundance, where an increase in agriculture around the fragment showed a decrease in bee abundance. *Ceratina* abundance decreased with an increase in patch size, which was also seen in *A. erigeniae. Ceratina* are pith nesters, so their abundance was predicted to be high with increasing

understory density, which could act as more nesting substrates. The relationship between decreasing abundance with increasing patch size might be a result of smaller fragments being more disturbed (and in an early successional state) and have a different floral composition than a fragment that is comprised more of canopy trees and native spring flowers. Early successional, smaller plots would typically be more heavily invaded with nonnative plants, which could have more nesting substrates compared to larger and established forests, which typically lack significant understory. The global model ranked as one of the highest models to best predict *Ceratina* abundance, suggesting that variables that were not studied may be influencing abundance more accurately than the studied variables.

1.4.4.4 Halictidae

Halictidae abundance was best predicted by understory density, where abundance decreased with increasing understory plants (Table 1.12). Like *Andrena*, Halictid bees are ground nesters, and their nesting abilities may be hampered by high understory density. Halictid abundance also decreased with an increase in tree density, suggesting that a high number of trees may outcompete the floral resources Halictids are searching for. The global model was the second best predicting model for abundance of Halictids, suggesting that variables not measured may be impacting abundance.

1.4.4.5 *Osmia*

The global model ranked as the best predictor of *Osmia* abundance (Table 1.13), which signifies that variables not being studied may be driving abundance of this genus. The two variables that were driving the global model were impervious

surface around the fragment and patch size, with an increase in abundance with an increase in both variables. *Osmia* do not create their own nests and instead nest in abandoned beetle burrows, old solitary bee tunnels, hollowed out sticks, etc.; therefore, impervious surface may contain a high number of these nesting substrates. *Osmia* also increased with an increase in patch size, which may be due to more available nesting substrates in larger forest patches. Surveying other nesting variables such as the amount of hollow twigs occupying forest fragments and using that as a covariate to predict *Osmia* abundance may prove more fruitful.

1.4.4.6 *Nomada*

Nomada abundance was best predicted by the landscape model, which included agriculture surrounding the site, impervious surface surrounding the site, and patch size (Table 1.14). Agriculture surrounding the site and patch size were highly influential in driving the landscape model to predict *Nomada* abundance negatively and positively, respectively. *Nomada* parasitize ground nesting bees such as *Andrena* and Halictidae by laying their eggs inside host brood cells. *Nomada* eggs hatch earlier than the host's egg, and the parasitic larvae kill the host larva and eat the provisioned pollen. Since *Nomada* do not build their own nests nor collect pollen, it is likely that they do not respond directly to site characteristics in the same way as other bee species, but instead may respond to the presence or absence of their hosts. Linear regression between *Nomada* and *Andrena* did not show a significant relationship between both genera, suggesting that *Nomada* may be opportunistic parasites or could be parasitizing other genera such as *Lasioglossum*. Additionally, our study along with other studies found that *Nomada* occur in high densities along forest edges in disturbed habitats (Bailey *et al.,* 2014). Further studies focusing on bee collections

using bowl traps in edge habitats and comparing species composition between edge habitats and interior forest may find differences in *Nomada* abundance.

1.4.5 Genetic analysis

Bombus impatiens and *Bombus bimaculatus* were both common species in and more often surrounding the study sites for both field seasons (2013-2014). Population genetic analyses did not reveal any population structure in *Bombus impatiens* sampled throughout the FRAME sites, and a lack of population structure in *B. impatiens* was found in previous studies as well (Lozier and Cameron, 2009). The program Structure and Structure Harvester found that samples of *B. bimaculatus* collected from FRAME sites represented two genetically distinct populations (Figure 1.19). This was further supported by the FCA analyses that shows little genetic overlap between *B. bimaculatus* sampled from Webb Farm versus other sites (Figure 1.18), and overlap between *B. impatiens* sampled in all sites but Reservoir (Figure 1.17). Both species showed high allelic richness throughout most sites (Table 1.15, 1.16), agreeing with previous research showing that *B. impatiens* has high genetic diversity Lozier *et al.,* 2011). Average and private allelic richness, after rarefaction, was variable between collection sites for both species (Table 1.15, 1.16). In *B. impatiens*, the bees collected from Reservoir were the most diverse in terms of private alleles and expected heterozygosity. This high level of diversity in bees sampled from Reservoir was also supported by the FCA analysis (as being genetically distinct from bees collected from other sites). *B. bimaculatus* had a higher number of private alleles and expected heterozygosity at White Clay, Webb Farm, and Chrysler Woods, which is supported by the Structure barplot as being genetically distinct from the other sites (Figure 1.19, Table 1.15), and the FCA analysis suggested that Webb Farm was genetically distinct

from bees collected from other sites. These results suggest that there lies some level of population structure at least in *B. bimaculatus*.

Differences in the genetic structuring of the two species suggest that *B. impatiens* and *B. bimaculatus* respond differently to habitat fragmentation. Studies have shown that *B. impatiens* gene diversity has not changed over temporal or spatial periods (Lozier and Cameron, 2009), and this species is found commonly throughout many ecosystems. This lack in genetic structure and high level of genetic diversity in common *Bombus* species has been shown in many landscapes unless the populations are geographically isolated (Widmer and Schmid-Hempel, 1999; Lozier *et al,* 2011). Studies; therefore, support the idea that *B. impatiens* can move and breed across environmental barriers. Not as much is known about the life history and population genetics of *B. bimaculatus*.

Forest fragmentation is thought to impact different bees at different rates, where some bees may function unchanged or more efficiently in a disturbed landscape, whereas others may decline. Studies on the genetic differentiation in two Euglossine species showed a correlation between genetic and geographic distance with one species but no correlation with another (Suni and Brosi, 2012). Euglossine bees are more specialized flower visitors, while *Bombus* spp. are more generalists and colonial; therefore, this study demonstrated the negative impacts fragmentation had on Euglossine populations. *Bombus* species, on the other hand, thrive in fragmented, semi-natural habitats with infrequent disturbances (Carvell *et al*., 2006) and may thrive in modestly disturbed areas like northern Delaware, which may explain why both species still had high allelic diversity.

Typically, low genetic diversity indicates that a species is already at risk; the species studied did not show low genetic diversity or noted population declines. Genetic isolation may only be seen when dealing with significant geographic isolation such as islands and large mountain ranges. Low population structure in collected bees may also be indicative of capturing sisters when collecting, which may skew population estimates. Polyandry has been shown to play a role in mating for both *B. impatiens* and *B. bimaculatus* (Payne *et al*., 2003), increasing their genetic diversity. Rare, monoandrous, and declining species may result in more inbreeding and lower genetic variation (Darvill *et al.,* 2006). *Bombus bimaculatus* may be more genetically isolated due to factors such as more restrictive diets, preferential nesting sites being harder to find, or dispersing queens may fly further distances compared to *B. impatiens*. Few studies focused on life history of both species and species-specific behavior is rarely noted in literature.

1.4.6 Pesticide analysis

Pesticide exposure in honey bees and native bee species has been a topic of concern in recent years; however, there still lacks ultimate results suggesting there are issues with the accuracy and feasibility of current assays to detect the impacts of pesticide exposure both acutely and chronically. Bee samples were compiled from six field sites from sweep netted bees and sent to a lab for pesticide analysis (Table 1.17). Most pesticide levels were near or below the limit of quantification and far from LD_{50} levels with the exception of Imidacloprid which has been shown to delay foraging, increase disappearance rates, and has been found in nectar and pollen collected by honey bees (Mullin *et al*., 2010). Flucythrinate I and II were found on bees from White Clay 1 and were nearly or above half of the recorded LD_{50} level for honey bees.

Studies investigating effects of pesticide exposure on native bees showed declines in adults and progeny and a male-biased offspring ratio (Alston *et al.*, 2007; Sandrock *et al*., 2014), while other studies found no correlations in honey bees (Chauzat *et al.*, 2009). Cognitive changes such as erratic behavior, interrupted foraging, and irregular nesting activity after exposure to pesticides has also been noted in *Osmia lignaria* (Ladumer *et al.*, 2008).

One site location, White Clay 1, tested positive for more pesticides compared to others. White Clay 1 is adjacent to a hay field that houses a diverse array of flowers and native bees throughout the summer. Pesticide use at this site is likely to be for hay production and may have devastating impacts on insects coming into contact with the flowers. Other sites have varying land-use surrounding them, such as forest, urban/suburban, agriculture, and home gardens where homeowners may use a variety of pesticides. Pesticide research is primarily focused on exposure to adults, brood, pollen and wax of honey bees; however, these samples are results from only adult native bees and the levels of pesticides in developing brood and pollen are expected to be different and likely at higher levels (Mullin *et al.,* 2010). Interestingly, DDT was found on bees in two particularly disturbed sites, Philips and Motorpool .A DDT metabolite (DDE) was found at all seven tested sites. Pesticide half-lives may play a huge role in the degree in which bees are exposed to chemicals, as DDT has a half-life of around 10 years. All LD_{50} levels given are for honey bees, therefore pesticide levels may have drastically different effects on other bees depending on their size, foraging behavior, and metabolism. Additionally, the presence of pesticides only alludes to how much pesticide the bee was exposed to ,and not the amount of pesticide they have been exposed to long-term. Most literature suggests the amount of a pesticide that will

kill insects, but sub-lethal doses and effects as well as the chronic, long-term effects of pesticide exposure to all insects is poorly studied. Generally, research on pesticide exposure to pollinators focuses solely on one compound, but realistically pollinators are contacting a suite of compounds that often times act synergistically.

1.4.7 Conclusions

Native bees as pollinators are an extremely important guild in the insect community, contributing crucial ecosystem services that support biodiversity. Our results indicate that a complex variety of factors support native pollinator populations. We saw that bees emerge at similar times regardless of weather conditions across two years, but their population sizes vary depending on the genus. Species richness varied between field sites, but showed no significant relationship with site characteristics, suggesting that factors not measured in this study may be driving species richness. Beta diversity was seen to vary depending on the field site, but there was no significant relationship between beta diversity and site characteristics. Generally, bee abundance was best predicted to decrease with an increase in agriculture surrounding the forest patch 1000 m from the field site. Other factors that highly predicted bee abundance included soil saturation, understory and tree density, and leaf litter. Genetic analyses conclude that two common bumble bee species (*Bombus impatiens* and *Bombus bimaculatus*) have different genetic structuring within the same forest patches, high allelic diversity; however, further predictions will require a larger sample size for more accurate results. Seventeen pesticides were detected in mostly low amounts in seven field sites, with many pesticides present on adult bees captured near a hay field. Long-scale monitoring of bees exposed to a variety of pesticides is crucial to assess chronic health changes. Continued research in areas such as floral

diversity, genetic diversity in both social and solitary native bees, and long-term pesticide exposure are important to assess the overall health of the native pollinator community.

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Appendix A

SUPPLEMENTARY GRAPHS

Table 1.18: Eight microsatellite markers used to test genetic diversity in *Bombus impatiens* and *Bombus bimaculatus* and their corresponding information (Jonathon Koch, personal communication). Tag: marker dye color, Range: range of microsatellite length in base pairs, Motif: core sequence, T: annealing temperature.

Marker	Tag	Range	Forward	Reverse	Motif	Motif count	T(°C)	Reference
B126	VIC-green	82-210	GCTTGCTGGTGAATTGTGC	CGATTCTCTCGTGTACTCC	CT	2	57	Estoup et al. 1995
BL11	PET-red	118-164	AAGGGTACGAAATGCGCGAG	TGACGAGTGCGGCCTTTTTC	TG	2	54	Funk 2006
B124	FAM-blue	216-280	GCAACAGGTCGGGTTAGAG	CAGGATAGGGTAGGTAAGCAG	CT,GC,GGCT	2,4	57	Estoup et al. 1995
BTMS59	PET-red	322-373	GGCTAGGAAAGATTAGCACTACC	AGTTCGACAGACCAAGCTGT	AGAC	4	60	Stolle 2009
BL13	PET-red	139-224	CGAGTAAGCTGCGTTTTGAATG	CTGAGCGTGTTATTTTCACGG	CA,AC	2	53	Funk 2006
BTMS62	VIC-green	210-316	CTGTCGCATTATTCGCGGTT	CTGGGCGTGATTCGATGAAC	CT	2	60	Stolle 2009
BTMS44	PET-red	239-328	AGGATCGAGAGAACGAGCTG	AGGCCTTGGGAGAGTTCG	GAG,CAC	3	60	STOLLE 2009
BTMS86	NED-yellow	255-330	AGAGAAATTGCATGCGGTCG	CTCGCGCTTGTCGAATCAAT	TCC	3	60	Stolle 2009

Table 1.19: All bees collected from bowl traps in northern Delaware (refer to Table 1.1 for site abbreviations). Values indicate mean number of bees collected during each visit (total of 18 visits), with the standard error in parentheses.

Species	CC2	CW	DM	EW	IH2	MCI	MP	PDW	PH	RE	RH	SL1	WC1	WF
Andrenidae														
***Andrena arabis* Robertson, 1897**	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.12)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena banksi* Malloch, 1917**	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.18)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena barbara* Bouseman and LaBerge, 1979**	0.19	0.07	0.00	0.07	0.06	0.13	0.00	0.00	0.20	0.13	0.00	0.00	0.36	0.08
	(0.10)	(0.06)	(0.00)	(0.06)	(0.06)	(0.08)	(0.00)	(0.00)	(0.10)	(0.08)	(0.00)	(0.00)	(0.15)	(0.07)
***Andrena bradleyi* Viereck, 1907**	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena carlini* Cockerell, 1901**	0.94	1.80	2.00	1.29	0.56	2.73	0.69	0.73	1.73	1.13	2.20	0.62	1.64	5.46
	(0.46)	(1.45)	(1.07)	(0.88)	(0.41)	(1.26)	(0.28)	(0.44)	(0.86)	(0.57)	(1.34)	(0.28)	(1.19)	(2.78)
***Andrena ceanothi* Viereck, 1917**	0.00	0.00	0.13	0.00	0.00	0.00	0.08	0.00	0.07	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.12)	(0.00)	(0.00)	(0.00)	(0.07)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena confederata* Viereck, 1917**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)
***Andrena cressonii* Robertson, 1891**	0.00	0.07	0.00	0.07	0.00	0.00	0.08	0.09	0.20	0.07	0.07	0.00	0.00	0.00
	(0.00)	(0.06)	(0.00)	(0.06)	(0.00)	(0.00)	(0.07)	(0.07)	(0.10)	(0.06)	(0.06)	(0.00)	(0.00)	(0.00)
***Andrena erigeniae* Robertson, 1891**	5.25	5.47	5.13	2.64	0.25	0.87	0.62	0.00	0.67	3.60	1.67	0.38	2.79	5.15
	(2.10)	(3.27)	(2.03)	(1.37)	(0.14)	(0.45)	(0.39)	(0.00)	(0.40)	(1.05)	(0.60)	(0.18)	(1.30)	(1.72)
***Andrena erythronii* Robertson, 1891**	0.00	0.00	0.31	0.00	0.00	0.07	0.00	0.00	0.07	0.00	0.07	0.00	0.00	0.00
	(0.00)	(0.00)	(0.24)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.06)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)
***Andrena fenningeri* Viereck, 1922**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena forbesii* Robertson, 1891**	0.00	0.00	0.25	0.00	0.13	0.00	0.15	0.00	0.00	0.00	0.20	0.08	0.07	0.00
	(0.00)	(0.00)	(0.24)	(0.00)	(0.12)	(0.00)	(0.13)	(0.00)	(0.00)	(0.00)	(0.18)	(0.07)	(0.06)	(0.00)
***Andrena heraclei* Robertson, 1897**	0.00	0.00	0.00	0.00	0.00	0.07	0.08	0.00	0.00	0.00	0.07	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.07)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)
***Andrena ilicis* Mitchell, 1960**	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.20)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena illini* Bouseman and LaBerge, 1979**	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.07	0.00	0.07	0.08
	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.06)	(0.00)	(0.06)	(0.07)
***Andrena imitatrix* Cresson, 1872**	0.00	0.00	0.00	0.00	0.06	0.07	0.08	0.00	0.00	0.07	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.06)	(0.07)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena imitatrix/morrisonelli* Viereck, 1917**	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00
	(0.00)	(0.10)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.08)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena krigiana* Robertson, 1901**	0.00	0.07	0.00	0.07	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00
	(0.00)	(0.06)	(0.00)	(0.06)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.07)	(0.00)	(0.00)
***Andrena macoupinensis* Robertson, 1900**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.07	0.15	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.06)	(0.13)	(0.00)	(0.00)

***Andrena mariae* Robertson, 1891**	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.07)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena milwaukeensis* Graenicher, 1903**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.20)	(0.00)	(0.00)
***Andrena miserabilis* Cresson, 1872**	0.06	0.07	0.06	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00
	(0.06)	(0.06)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena morrisonella* Viereck, 1917**	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena nasonii* Robertson, 1895**	0.06	0.00	0.06	0.14	0.00	0.13	0.08	0.27	0.00	0.13	0.07	0.08	0.86	0.08
	(0.06)	(0.00)	(0.06)	(0.09)	(0.00)	(0.12)	(0.07)	(0.11)	(0.00)	(0.08)	(0.06)	(0.07)	(0.43)	(0.07)
***Andrena nigrihirta* (Ashmead, 1890)**	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena nivalis* Smith, 1853**	0.06	0.13	0.50	0.00	0.13	0.00	0.00	0.00	0.73	0.00	0.13	0.62	0.64	0.31
	(0.06)	(0.12)	(0.31)	(0.00)	(0.08)	(0.00)	(0.00)	(0.00)	(0.49)	(0.00)	(0.12)	(0.46)	(0.57)	(0.20)
***Andrena nuda* Robertson, 1891**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.60)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena perplexa* Smith, 1853**	0.00	0.13	0.06	0.14	0.38	0.13	0.15	0.45	0.07	0.27	0.20	0.00	0.21	0.00
	(0.00)	(0.08)	(0.06)	(0.13)	(0.15)	(0.08)	(0.13)	(0.29)	(0.06)	(0.14)	(0.13)	(0.00)	(0.10)	(0.00)
***Andrena personata* Robertson, 1897**	0.06	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.07	0.07	0.07	0.00	0.07	0.00
	(0.06)	(0.00)	(0.18)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.06)	(0.06)	(0.00)	(0.06)	(0.00)
***Andrena phaceliae* Mitchell, 1960**	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena pruni* Robertson, 1891**	0.06	0.00	0.63	0.29	0.19	0.33	0.00	0.18	0.07	1.40	0.47	0.15	0.93	0.62
	(0.06)	(0.00)	(0.36)	(0.19)	(0.13)	(0.25)	(0.00)	(0.10)	(0.06)	(1.15)	(0.37)	(0.09)	(0.47)	(0.31)
***Andrena robertsonii* Dalla Torre, 1896**	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.14	0.15
	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.09)	(0.13)
***Andrena spiraeana* Robertson, 1895**	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Andrena tridens* Robertson, 1902**	0.06	0.00	0.06	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.07	0.08	0.21	0.00
	(0.06)	(0.00)	(0.06)	(0.00)	(0.12)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.07)	(0.10)	(0.00)
***Andrena vicina* Smith, 1853**	0.19	0.00	0.13	0.21	0.00	0.00	0.15	0.00	0.00	0.33	0.00	0.08	0.36	0.23
	(0.10)	(0.00)	(0.08)	(0.10)	(0.00)	(0.00)	(0.09)	(0.00)	(0.00)	(0.19)	(0.00)	(0.07)	(0.25)	(0.14)
***Andrena violae* Robertson, 1891**	0.06	0.60	1.19	0.36	0.69	0.33	0.08	1.09	0.47	1.00	0.87	0.00	2.07	0.23
	(0.06)	(0.43)	(0.76)	(0.18)	(0.32)	(0.19)	(0.07)	(0.78)	(0.22)	(0.44)	(0.38)	(0.00)	(0.93)	(0.14)
***Andrena virginiana* Mitchell, 1960**	0.00	0.07	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00
	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)
***Andrena wheeleri* Graenicher, 1904**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)
***Andrena ziziaeformis* Cockerell, 1908**	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Apidae														
***Apis mellifera* Linnaeus, 1758**	0.00	0.07	0.06	0.07	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.07	0.00
	(0.00)	(0.06)	(0.06)	(0.06)	(0.00)	(0.00)	(0.00)	(0.07)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)
***Bombus bimaculatus* Cresson,**	0.06	0.00	0.00	0.00	0.06	0.07	0.08	0.18	0.07	0.07	0.07	0.00	0.07	0.08

1863	(0.06)	(0.00)	(0.00)	(0.00)	(0.06)	(0.06)	(0.07)	(0.10)	(0.06)	(0.06)	(0.06)	(0.00)	(0.06)	(0.07)
***Bombus griseocollis* (DeGeer, 1773)**	0.00	0.00	0.06	0.00	0.00	0.00	0.08	0.00	0.07	0.00	0.07	0.00	0.00	0.00
	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.07)	(0.00)	(0.06)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)
***Bombus impatiens* Cresson, 1863**	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.10)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Bombus perplexus* Cresson, 1863**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)
***Ceratina calcarata* Robertson, 1900**	2.69	0.80	0.75	0.29	0.00	0.13	1.15	0.55	0.93	1.00	0.13	0.08	0.14	0.31
	(1.28)	(0.40)	(0.36)	(0.19)	(0.00)	(0.12)	(0.39)	(0.24)	(0.47)	(0.45)	(0.08)	(0.07)	(0.13)	(0.15)
***Ceratina dupla* Say, 1837**	0.25	0.00	0.00	0.07	0.06	0.00	0.15	0.00	0.13	0.13	0.00	0.00	0.00	0.00
	(0.11)	(0.00)	(0.00)	(0.06)	(0.06)	(0.00)	(0.09)	(0.00)	(0.12)	(0.08)	(0.00)	(0.00)	(0.00)	(0.00)
***Ceratina strenua* Smith, 1879**	0.50	0.00	0.00	0.14	0.06	0.00	0.46	0.00	0.40	0.07	0.00	0.00	0.07	0.08
	(0.15)	(0.00)	(0.00)	(0.13)	(0.06)	(0.00)	(0.23)	(0.00)	(0.21)	(0.06)	(0.00)	(0.00)	(0.06)	(0.07)
***Nomada armatella* Cockerell, 1903**	0.06	0.00	0.00	0.00	0.06	0.27	0.00	0.00	0.07	0.00	0.07	0.00	0.79	0.00
	(0.06)	(0.00)	(0.00)	(0.00)	(0.06)	(0.24)	(0.00)	(0.00)	(0.06)	(0.00)	(0.06)	(0.00)	(0.47)	(0.00)
***Nomada composita* Mitchell, 1962**	0.06	0.07	0.06	0.00	0.06	0.13	0.00	0.00	0.00	0.33	0.07	0.08	0.07	0.00
	(0.06)	(0.06)	(0.06)	(0.00)	(0.06)	(0.12)	(0.00)	(0.00)	(0.00)	(0.30)	(0.06)	(0.07)	(0.06)	(0.00)
***Nomada cressonii* Robertson, 1893**	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Nomada denticulata* Robertson, 1902**	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Nomada depressa* Cresson, 1863**	0.13	0.07	0.56	0.07	1.63	0.20	0.85	0.18	0.27	0.60	0.60	0.08	1.14	0.31
	(0.12)	(0.06)	(0.35)	(0.06)	(0.94)	(0.10)	(0.72)	(0.10)	(0.14)	(0.43)	(0.33)	(0.07)	(0.70)	(0.20)
***Nomada gracilis* Cresson, 1863**	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.15
	(0.12)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.12)	(0.00)	(0.00)	(0.13)
***Nomada imbricata* Smith, 1854**	0.00	0.00	0.38	0.00	0.63	0.00	0.08	0.09	0.00	0.00	0.47	0.15	0.00	0.00
	(0.00)	(0.00)	(0.24)	(0.00)	(0.37)	(0.00)	(0.07)	(0.07)	(0.00)	(0.00)	(0.22)	(0.09)	(0.00)	(0.00)
***Nomada lehighensis* Cockerell, 1903**	0.00	0.00	0.13	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00
	(0.00)	(0.00)	(0.12)	(0.00)	(0.08)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)
***Nomada luteoloides* Robertson, 1895**	0.06	0.13	1.38	0.14	0.75	0.27	0.38	0.18	0.93	0.53	1.00	0.08	2.64	0.69
	(0.06)	(0.12)	(0.60)	(0.09)	(0.33)	(0.14)	(0.20)	(0.10)	(0.56)	(0.25)	(0.53)	(0.07)	(1.33)	(0.39)
***Nomada maculata* Cresson, 1863**	0.06	0.00	0.00	0.14	0.00	0.33	0.00	0.00	0.00	0.13	0.00	0.00	0.14	0.00
	(0.06)	(0.00)	(0.00)	(0.09)	(0.00)	(0.30)	(0.00)	(0.00)	(0.00)	(0.08)	(0.00)	(0.00)	(0.13)	(0.00)
***Nomada obliterata* Cresson, 1863**	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.07)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
***Nomada pygmaea* Cresson, 1863**	0.06	0.60	0.25	0.07	0.50	0.07	0.00	0.09	0.27	0.33	0.27	0.00	0.36	0.54
	(0.06)	(0.26)	(0.14)	(0.06)	(0.21)	(0.06)	(0.00)	(0.07)	(0.14)	(0.15)	(0.11)	(0.00)	(0.15)	(0.23)
***Nomada sayi/illinoensis* Robertson, 1893**	0.00	0.07	0.06	0.14	0.00	0.00	0.00	0.18	0.00	0.07	0.07	0.00	0.00	0.00
	(0.00)	(0.06)	(0.06)	(0.13)	(0.00)	(0.00)	(0.00)	(0.10)	(0.00)	(0.06)	(0.06)	(0.00)	(0.00)	(0.00)
***Nomada sulphurata* Smith, 1854**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.13)	(0.00)
Colletidae														
***Colletes inaequalis* Say, 1837**	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.12)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)

***Hylaeus illinoisensis* (Robertson, 1896)**	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.07 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Halictidae														
***Agapostemon virescens* (Fabricius, 1775)**	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.13 (0.08)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.07 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
***Augochlora pura* (Say, 1837)**	0.06 (0.06)	0.07 (0.06)	0.13 (0.08)	0.00 (0.00)	0.25 (0.14)	0.07 (0.06)	0.08 (0.07)	0.00 (0.00)	0.40 (0.31)	1.07 (0.48)	0.13 (0.08)	0.00 (0.00)	0.29 (0.19)	0.08 (0.07)
***Augochlorella aurata* (Smith, 1853)**	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.06 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
***Augochloropsis metallica* (Fabricius, 1793)**	0.06 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.07 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.07 (0.06)	0.00 (0.00)	0.07 (0.06)	0.00 (0.00)
***Halictus confusus* Smith, 1853**	0.06 (0.06)	0.00 (0.00)	0.06 (0.06)	0.00 (0.00)	0.00 (0.00)	0.47 0.29)	0.00 (0.00)	0.09 (0.07)	0.33 (0.25)	0.00 (0.00)	0.13 (0.08)	0.00 (0.00)	0.29 (0.19)	0.00 (0.00)
***Halictus ligatus/poeyi* Say, 1837**	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.08 (0.07)
***Halictus rubicundus* (Christ, 1791)**	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.13 (0.12)	0.00 (0.00)	0.08 (0.07)	0.00 (0.00)	0.00 (0.00)
***Lasioglossum birkmanni* (Crawford, 1906)**	0.06 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.08 (0.07)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
***Lasioglossum cattellae* (Ellis, 1913)**	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.07 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
***Lasioglossum coeruleum* (Robertson, 1893)**	0.00 (0.00)	0.00 (0.00)	0.13 (0.08)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.23 (0.14)	0.07 (0.06)	0.00 (0.00)
***Lasioglossum coriaceum* (Smith, 1853)**	0.06 (0.06)	0.00 (0.00)	0.06 (0.06)	0.00 (0.00)	0.06 (0.06)	0.00 (0.00)	0.08 (0.07)	0.18 (0.10)	0.07 (0.06)	0.00 (0.00)	0.20 (0.13)	0.15 (0.09)	0.07 (0.06)	0.00 (0.00)
***Lasioglossum cressonii* (Robertson, 1890)**	0.06 (0.06)	0.00 (0.00)	0.00 (0.00)	0.07 (0.06)	0.06 (0.06)	0.07 (0.06)	0.15 (0.13)	0.00 (0.00)	0.07 (0.06)	0.40 (0.17)	0.20 (0.10)	0.00 (0.00)	0.07 (0.06)	0.08 (0.07)
***Lasioglossum foxii* (Robertson, 1895)**	0.00 (0.00)	0.00 (0.00)	0.06 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
***Lasioglossum fuscipenne* (Smith, 1853)**	0.00 (0.00)	0.07 (0.06)	0.06 (0.06)	0.00 (0.00)	0.06 (0.06)	0.00 (0.00)	0.08 (0.07)	0.09 (0.07)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.08 (0.07)	0.00 (0.00)	0.00 (0.00)
***Lasioglossum gotham* Gibbs 2011**	0.13 (0.08)	0.13 (0.08)	0.63 (0.42)	0.00 (0.00)	0.44 (0.30)	0.00 (0.00)	0.77 (0.46)	0.00 (0.00)	1.07 (0.91)	0.73 (0.55)	0.60 (0.31)	0.08 (0.07)	0.00 (0.00)	0.77 (0.65)
***Lasioglossum hitchensi* Gibbs 2012**	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.07 (0.06)	0.00 (0.00)
***Lasioglossum illinoense* (Robertson, 1892)**	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.06 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.07 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
***Lasioglossum imitatum* (Smith, 1853)**	0.00 (0.00)	0.00 (0.00)	0.06 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.13 (0.08)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
***Lasioglossum oblongum* (Lovell, 1905)**	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.13 (0.12)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
***Lasioglossum obscurum* (Robertson, 1892)**	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.07 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
***Lasioglossum pilosum* (Smith,**	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

1853)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Lasioglossum quebecense	0.00	0.00	0.13	0.43	0.00	0.33	0.00	2.09	0.00	0.33	0.20	0.00	0.86	0.00
(Crawford, 1907)	(0.00)	(0.00)	(0.08)	(0.22)	(0.00)	(0.25)	(0.00)	(1.48)	(0.00)	(0.25)	(0.13)	(0.00)	(0.44)	(0.00)
Lasioglossum smilacinae	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(Robertson, 1897)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Lasioglossum subviridatum	0.25	0.93	0.44	0.86	1.94	2.07	0.31	1.64	0.80	5.80	0.87	0.23	1.21	0.15
(Cockerell, 1938)	(0.11)	(0.48)	(0.17)	(0.43)	(0.80)	(1.20)	(0.11)	(0.71)	(0.34)	(2.30)	(0.47)	(0.14)	(0.55)	(0.09)
Lasioglossum versatum	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00
(Robertson, 1902)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Lasioglossum weemsi **(Mitchell,**	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1960)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Sphecodes coronus **Mitchell, 1956**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.15
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.12)	(0.00)	(0.00)	(0.00)	(0.00)	(0.13)
Sphecodes galerus **Lovell and**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00
Cockerell, 1907	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)
Sphecodes illinoensis **(Robertson,**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00
1903)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)
Sphecodes mandibularis **Cresson,**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00
1872	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)
Sphecodes ranunculi **Robertson,**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00
1897	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Megachilidae														
Osmia atriventris **Cresson, 1864**	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.08)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Osmia bucephala **Cresson, 1864**	0.06	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.07	0.00	0.00	0.00	0.00	0.00
	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.09)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Osmia collinsiae **Robertson, 1905**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.09)	(0.00)	(0.00)	(0.00)	(0.00)
Osmia cornifrons **(Radoszkowski,**	0.25	0.47	0.06	0.00	0.56	0.07	0.08	0.09	0.53	0.00	0.13	0.23	0.36	0.23
1887)	(0.18)	(0.23)	(0.06)	(0.00)	(0.32)	(0.06)	(0.07)	(0.07)	(0.29)	(0.00)	(0.12)	(0.20)	(0.31)	(0.14)
Osmia georgica **Cresson, 1878**	0.44	0.33	0.19	0.00	0.31	0.07	0.00	0.00	0.13	0.07	0.07	0.46	0.07	0.23
	(0.21)	(0.25)	(0.13)	(0.00)	(0.17)	(0.06)	(0.00)	(0.00)	(0.08)	(0.06)	(0.06)	(0.39)	(0.06)	(0.10)
Osmia lignaria **Say, 1837**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.13	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.08)	(0.00)	(0.00)	(0.00)	(0.00)
Osmia pumila **Cresson, 1864**	0.38	0.53	0.38	0.43	0.81	0.00	0.38	0.91	2.20	0.40	0.80	0.54	0.29	0.08
	(0.24)	(0.29)	(0.24)	(0.26)	(0.55)	(0.00)	(0.20)	(0.64)	(1.03)	(0.20)	(0.55)	(0.27)	(0.14)	(0.07)
Osmia taurus **Smith, 1873**	0.94	0.60	0.13	0.29	0.88	0.27	0.08	0.64	0.27	0.13	0.73	0.77	2.00	0.15
	(0.44)	(0.28)	(0.08)	(0.25)	(0.51)	(0.19)	(0.07)	(0.37)	(0.19)	(0.08)	(0.30)	(0.45)	(1.46)	(0.13)

Table 1.20: Flowers visited by bees, separated by pollinator genus, 2013 and 2014 collectively. Flower names are ordered from most commonly to least commonly visited within each bee genus.

Andrena	***Bombus***	***Ceratina***	***Lasioglossum***	***Nomada***	***Osmia***
Claytonia virginica (L.)	*Securigera varia* (L.) Lassen	*Claytonia virginica* (L.)	*Claytonia virginica* (L.)	*Cirsium arvense* (L.) Scop.	*Trifolium hybridum* L.
Viburnum sp.	*Trifolium repens* L.	*Alliaria petiolata* (M. Bieb.)	*Cirsium arvense* (L.) Scop.	*Claytonia virginica* (L.)	*Viburnum sp.*
Cirsium arvense (L.) Scop.	*Daucus carota* L.	*Rosa multiflora* Thunb.	*Rosa multiflora* Thunb.	*Viburnum sp.*	*Pieris japonica* (Thunb.) D. Don ex G. Don
Rosa multiflora Thunb.	*Ranunculus sp.*	*Chicorium intybus* L.	*Alliaria petiolata* (M. Bieb.)	*Eutrochium sp.*	*Trifolium repens* L.
Trifolium hybridum L.	*Rubus occidentalis* L.	*Hibiscus moscheutos* L.	*Viburnum sp.*	*Glycine max* (L.) Merr.	*Calystegia seplum* (L.) R. Br.
Chicorium intybus L.	*Sinapis arvensis* L.	*Viburnum sp.*	*Trifolium hybridum* L.	*Hemerocallis sp.*	*Claytonia virginica* (.)
Circaea sp.	*Calystegia seplum* (L.) R. Br.	*Pulicaria dysenterica* (L.) Bernh	*Chicorium intybus* L.	*Circaea sp.*	*Rubus sp.*
Pieris japonica (Thunb.) D. Don ex G. Don	*Elaeagnus umbellate* Thunb.	*Trifolium repens* L.	*Asclepias syriaca* L	*Apocynum sp.*	*Taraxicum sp.*
Securigera varia (L.) Lassen	*Chicorium intybus* L.	*Securigera varia* (L.) Lassen	*Veronicastrum virginicum* (L.) Farw.	*Hibiscus moscheutos* L.	
Eutrochium sp.	*Malus sp.*	*Digitalis purpurea* L.	*Erythronium sp.*		
Rudbeckia hirta L.	*Alliaria petiolata* (M. Bieb.)	*Solidago juncea* Ait.	*Trifolium repens* L.		
Veronicastrum virginicum (L.) Farw.	*Eutrochium sp.*	*Lonicera* japonica Thunb.	*Mertensia virginica* (L.)		
Trifolium pratense L.	*Trifolium pratense* L.	*Eutrochium sp.*	*Securigera varia* (L.) Lassen		
Elaeagnus umbellate Thunb.	*Trifolium hybridum* L.	*Pulicaria dysenterica* (L.) Bernh.	*Taraxicum sp.*		
Rubus occidentalis L.	*Rosa multiflora* Thunb.				
Sinapis arvensis L.	*Erythronium sp.*				
Calystegia seplum (L.) R. Br.	*Viburnum dentatum* L.				
Solanum sp.	*Viburnum prunifolium* L.				
Apocynum sp.	*Sanguinaria Canadensis* L.				

Hibiscus moscheutos L.	*Cirsium arvense* (L.) Scop.
Prunus sp.	*Pulicaria dysenterica* (L.) Bernh.
Ranunculus sp.	*Hibiscus moscheutos* L.
Asclepias syriaca L.	*Senna sp*.
Erigeron annuus (L.) Pers.	*Anemone sp*.
Solidago juncea Ait.	*Prunus sp*.
Lamium sp.	*Potenilla sp*.
Glycine max (L.) Merr.	*Cardamine concatenate* (Michx.) O. Schwars.
Daucus carota L.	*Solidago juncea* Ait.
Senna sp.	*Viburnum sp*.
Leucanthemum vulgare Lam.	*Lonicera* japonica Thunb.