WOODLAND BEE DIVERSITY IN THE MID-ATLANTIC

by

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ABSTRACT

Native bees are vital to both agricultural and natural systems for the valuable pollination services they provide. Honey bee colony losses have raised concerns over whether native pollinators are also at risk, and declines have been recorded in several species. However, the population status of most bee species remains unknown due to a lack of both historic and recent survey data, making it difficult to judge how bees are responding to habitat loss and other anthropogenic disturbances. The bulk of data has been collected in agricultural systems or open habitats, with forested areas rarely being surveyed for native bees.

In an effort to establish a baseline dataset for monitoring of forest bee communities, we surveyed vernal bees from woodlands across the Mid-Atlantic. We found a community dominated by solitary, ground nesting species, primarily in the genera *Andrena*, *Nomada*, *Osmia* and *Lasioglossum*. One new state record was collected in Maryland, *Andrena rufosignata*. Additionally, several species previously considered uncommon in the region were prevalent in the forest community, suggesting that sampling bias towards open habitats has resulted in under-sampling of bees closely associated with woodlands.

Sites differed in density of bees and species composition, but a typical list of forest bees emerged from our surveys. The most familiar faces in these communities are a few common *Andrena* species, *Andrena* carlini and *Andrena* perplexa, as well as the oligolectic Spring Beauty bee, *Andrena* erigeniae. The nest parasites of *Andrena*, species in the genus *Nomada*, are also usually present, as are a group of *Lasioglossum* species that seem to be associated with woodlands. Many of these forest dwelling species appear to be resilient to urban development; even our smallest forest fragments

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surrounded by dense urban development support many of these woodland associated bee species.

The results of our occupancy and abundance modeling were also promising for the conservation of bees in urban areas, with development rarely being a major landscape predictor. Instead, most species seem to prefer bottomland woodlands with some penetration of wetlands or open water over extensive closed canopy forest. These wetland and riparian areas create more open canopy forests that are likely to be rich in the vernal forbs and flowering woody plants wild bees forage on.

The results of our study offer a closer look into the forest bee community, how that community shifts across the landscape, and how species differ in their response to surrounding landcover. Our dataset can serve as a baseline for future monitoring of bees throughout the region, and the patterns that emerged will hopefully spur further investigation toward understanding wild pollinator ecology and population dynamics.

Chapter 1

MID-ATLANTIC WOODLAND BEE COMMUNITY

1.1 Introduction

1.1.1 Background

Pollination is an ecosystem service benefiting not only agriculture, but the integrity of natural systems as well. Most flowering plants rely on or benefit from animal pollinators (Ollerton et al. 2011), making pollinators integral to the health of the plant community and, subsequently, higher trophic levels. Just as plant communities shift across different habitat types, so do the suites of pollinators associated with them. Studying the pollinator community of a natural area is basal to understanding the ecosystem's function, health and management needs.

Bees are the most important animal pollinators, but there is insufficient data to judge the population status of most North American bee species. Declines have been documented in some commercially important species, particularly the domesticated European honey bee, *Apis mellifera*, (Holden 2006; National Research Council 2007; Aizen and Harder 2009; Meixner and Le Conte 2016), as well as a number of bumble bee species (Grixti et al. 2008; Colla and Packer 2008; Cameron et al. 2011). Just this year, the Rusty Patch Bumble Bee (*Bombus affinis*) became the first bee species in the continental U.S. to be protected under the Endangered Species Act (U.S. Fish and Wildlife 2017). Documentation of decline in *Apis* and *Bombus*, as opposed to other bee genera, is likely due to the larger volume of data on these species resulting from

commercial interests and their overall recognizability. Loss of a large, easily identified bumble bee species is more likely to be noted and investigated than that of a small, clandestine bee species.

However, this does not mean that trends in eusocial species can be extrapolated to infer the population status of the thousands of solitary bee species. Response to the stressors impacting *Apis* and *Bombus* (e.g habitat loss and degradation, pesticides, pathogens or parasites) likely varies species to species, with some bees capable of persisting in small natural remnants or even preferring heterogeneous, human dominated landscapes. Baseline data on population size and distribution for the majority of bee species is very limited (National Academy of Sciences 2007), precluding any inferences on population changes over time. Increasing the number of bee surveys on regional scales rather than at discreet locations would greatly improve our ability to monitor changes in distributions over time. Most studies of native bee diversity to date have been focused on fauna in or bordering agricultural fields from a perspective of promoting crop pollinators, and surveys in natural areas have focused on open habitats. Vernal bee communities in forests have been sampled rarely, and never on a regional scale.

Prior to European settlement, the landcover in Eastern North America was predominately forest (Yahner 2000). Native Americans periodically burned the understory, resulting in open woodlands with numerous tree gaps (Yahner 2000) that would have provided ideal habitat for bees. Bee communities likely shifted as Europeans cleared land for agriculture in the 19th century, but reforestation of former crop lands in the early 20th century actually increased forest cover in the Eastern US (Yahner 2000), and forest remains an important habitat for much of our eastern bee

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fauna. Trees are some of the first plants to flower in early spring, and beekeepers tout their importance as an early pollen source for honey bees (Hill and Webster 1995). Floral resources in forests are most abundant in spring before canopy closure, when sunlight still penetrates to the forest floor (Motten 1986). Early emerging wild bees are active in forests during this brief window, after which they either move to more open habitats or are dormant until the following year.

Temperate forests have been largely overlooked as pollinator habitat, and the bees closely tied to wooded areas remain under studied. Motten (1986) conducted a detailed study of the pollination systems in lowland forest sites within 12km of Duke University in North Carolina. The study identified some of the most visited forest flowers by bees (e.g. *Erythronium umbilicatum, Claytonia virginica, Cardamine angustata* and *Stellaria pubera*), noting that despite the short phenology and overlap in bloom period for these plants, sufficient pollination was achieved primarily by visitation of a variety of generalist pollinators. While some bee species exhibit strong preferences in floral hosts, the majority of both forest flowers and pollinators employ a generalist strategy, each relying on the ephemeral abundance of the other during the brief window before canopy closure.

Even after understory flowers have ceased blooming, the forest canopy may remain an important source of carbohydrates for many bee species. A study by Yshen et al. (2010) in Georgia compared the distribution of bees in the forest understory and canopy, finding high abundance in the canopy after mid-May (approximately the time of full canopy closure). The authors suggest these canopy bees are foraging for nonfloral sugar sources, such as honeydew, sap, and leaf nectaries, and likely travel to other habitats to gather pollen.

Closed canopy forest tends to have lower bee diversity than more open forests and suburban areas with moderate development, and gardens in suburban areas which can serve as quality habitat for a diverse bee community (Winfree et al. 2007; Grundel et al. 2010; Carper et al. 2014). These higher diversity measurements in disturbed, heterogenous habitat may be due to edge effects, with open habitat associated bees infiltrating forest edges to take advantage of early spring blooms. However, some species are closely associated with forests and may be rarely encountered outside of woodlands. Despite finding that overall bee diversity declined with increasing forest cover on the landscape scale, Winfree et. al (2007) identified a list of 18 species (representing 9 different genera) that were positively associated with forest cover. One of these, *Colletes bradleyi*, had only two previous records in New Jersey. Likewise, a survey of woodland bees in Maryland by Droege (2013) found that a number of previously thought uncommon species were abundant in these sites, despite intensive sampling of other habitats in the area. The paucity of bee surveys in extensive forest has undoubtedly led to forest habitat specialists being under sampled, and more of these species are sure to be identified if sampling efforts are increased in wooded areas.

Better characterizing the North American forest bee community will require that more attention be given to sampling bees in different forest types and regions across the continent. Basic survey data not only provides valuable information on the distributions, ranges and habitat use of species, but also provides a baseline demographic for monitoring purposes. Seeing this need, federal agencies and conservation groups have begun looking for simple and cost-effective monitoring protocols for bees. Using the inexpensive cup trap method piloted in the Droege

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(2013) study, we implemented a regional scale survey by recruiting citizen scientists to establish bee cup transects in forests across the Mid-Atlantic. Our survey outlines a strategy for large-scale bee monitoring with minimal costs and training effort, and adds a much-needed database of forest bee distributions in the region.

1.1.2 Objectives

The objectives of this study are to 1) demonstrate a cost-effective protocol for large-scale sampling and monitoring of native bees by relying on volunteers, 2) establish baseline data on bees in forested habitats in the Mid-Atlantic which can be compared to future surveys for the purpose of monitoring bee populations, 3) characterize the community of bees foraging in wooded areas and explore their ecology, diversity and phenology.

1.2 Methods

1.2.1 Study Area

Bees were sampled from 106 forested sites across Maryland, Delaware, Washington D.C. and Fairfax and Virginia Beach counties, Virginia. Of these sites, 103 sites were sampled in 2014, 42 sites were sampled in 2015, and 37 sites were sampled in both years (Fig. 1.1). Bee samples were collected by a network of volunteers, including some federal and state park employees, members of beekeeping and gardening groups and additional individuals found through snowball recruitment.

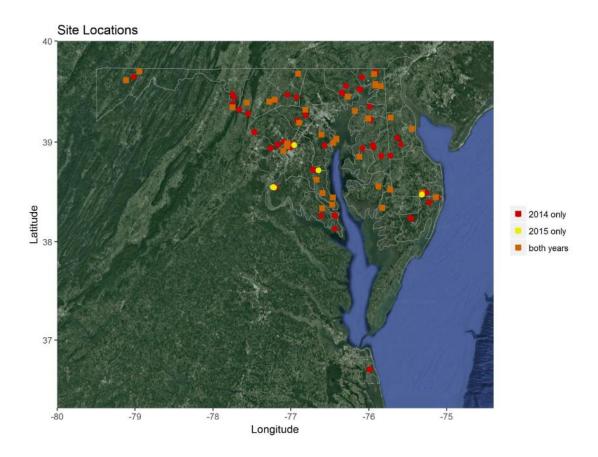


Figure 1.1: Map of all sites locations. Sites marked in red were sampled only in 2014, yellow only 2015 and orange sites were sampled in both years.

To maximize diversity in geographic area and forest type, our goal in 2014 was to recruit volunteers to run five transects in each county, with those five sites to include at least one young forest, one bottomland forest, and one acidic heath forest. While these criteria were not met for every county, this framework helped us establish a set of survey sites on both public and private lands, spanning the targeted region and representing a variety of forest types in terms of patch size, surrounding land use, land use history, and geographic region. A table of all sites, locations and years sampled can be found in Appendix A.

1.2.2 Cup Trapping Protocol

Bees were sampled using a simple cup trap method designed by Sam Droege (Droege, 2013). Each volunteer received nine 12oz plastic cups: 3 unpainted white, 3 painted fluorescent blue and 3 painted fluorescent yellow (Fig. 1.2; paints were ordered from Guerra Paints, colors "Fluorescent Yellow" and "Fluorescent Blue"). Also supplied were PVC stands to prevent cups from tipping, 1 gallon food grade propylene glycol, paint strainers, whirl packs and a datasheet.



Figure 1.2: Cup trap design A) Cups were painted fluorescent blue, fluorescent yellow or left white. B) PVC stands were used to prevent cups from tipping C) Insects were removed by pouring cups through a paint strainer.

Volunteers were asked to set their cup transect along the forest floor at least 30m from the forest edge with cups spaced approximately 10m apart. In both years,

transects were set in mid-March (approximately March 11) once spring temperatures reached 50°F. Each cup was filled 7/8 full with 50% propylene glycol in water and a small amount of unscented dish soap (such as blue Dawn soap) to reduce surface tension. Volunteers checked their trap transects weekly, recording the dates of collection and any additional notes on the datasheets provided. A single weekly collection consisted of pouring all contents of the nine cups through a single paint strainer, which was placed into a whirl pack with a label and frozen. By having volunteers collect all bycatch, rather than only saving bees, we eliminated user error related to differences in familiarity with bee taxa among our citizen scientists.

Weekly collections continued until volunteers reported no longer seeing bees in their traps, which was mid- to late-May in most sites. Some volunteers continued collecting into early June, but at most sites few or no bees were collected this late in the season. At the end of the collecting season we gathered all frozen samples and datasheets from volunteers and brought them to the USGS Bee Monitoring and Inventory lab in Beltsville, MD for processing and identification. Wherever possible, bees were identified to species, though there were some cases where specimens could only be identified to genus or subgenus, or where a pair or group of species could not be differentiated. In all analyses, only distinct species or groups of species are included. (For example, specimens identified to *Andrena* sp. were included in genus level estimates but were not counted as a unique species due to possible redundancy). All data were entered into a database hosted by DiscoverLife (*www.discoverlife.org*) and are publicly accessible through the DiscoverLife website.

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1.2.3 Analysis of Bee Community Data

Landcover variables were measured in ArcMap (10.2.2) using the National Landcover Dataset (US Geological Survey 2011). Landcover classes were grouped into: "Forest" (Deciduous Forest, Evergreen Forest and Mixed Forest); "Woody Wetlands", "Open" (Grassland/Herbaceous, Pasture/Hay, Developed Open Space, Shrub/Scrub and Cultivated Crops); "Wetland" (Emergent Herbaceous Wetland and Open Water); and "Developed" (Developed Low Intensity, Developed Medium Intensity and Developed High Intensity). Elevation for all sites was obtained using the R package "raster," and daily weather variables (temperature, precipitation, humidity, wind speed were pulled from the weather station nearest each sampling location using the R package "weatherdata" and averaged across each sampling week. For some analyses, bees were grouped into ecological guilds based on life history characteristics (these details can be found in Appendix B.1). In cases where these life history traits are unknown, they were inferred from closely related species. Mean abundance for ecological guild and phenology plots was calculated as the mean per site, treating sites sampled both years separately. Plots were made using R package "ggplot2" (Wickham 2009). Diversity indices and NMDS ordination were performed using the R package "vegan" (Oksanen et al. 2017) Shannon Diversity Index for each site was measured using the function "diversity." We used the functions "decostand" and "metaNMDS to measure Hellinger transformed Euclidean distance and perform non-metric multidimensional scaling analysis of genus level data for all sites.

1.3 Results and Discussion

1.3.1 Range of site level variables

All transects were set in deciduous or mixed forest, which varied in forest area and surrounding land use. Some sites were large state forests (eg Elk Neck State Forest in MD), while others were tiny forest patches in urban areas (eg. Fort Slocum and Fort Totten Parks in Washington D.C.). A tables of all sites and their landcover compositions can be found in Appendix A. Percent cover of forest within 1000m around the transect ranged from less than 2% to 92% (Fig. 1.3A), with percent developed in the urban sites reaching as much as 98% (Fig. 1.3E). The majority of sites had less than 25% woody wetland cover within 1000m, but in some sites the landcover was 100% woody wetland (Fig. 1.3B). Cover of open habitat ranged from 0% to 95% within 1000m (Fig. 1.3D). The majority of sites had less than 50% wetland and water within 1000m (Fig. 1.3C). By sampling across coastal plain, piedmont and mountains we were able to span a range of elevations. The majority of sites fell between 0 and 200m above sea level, with the few sites in Garrett Co., MD at 700-850m (Fig. 1.3F).

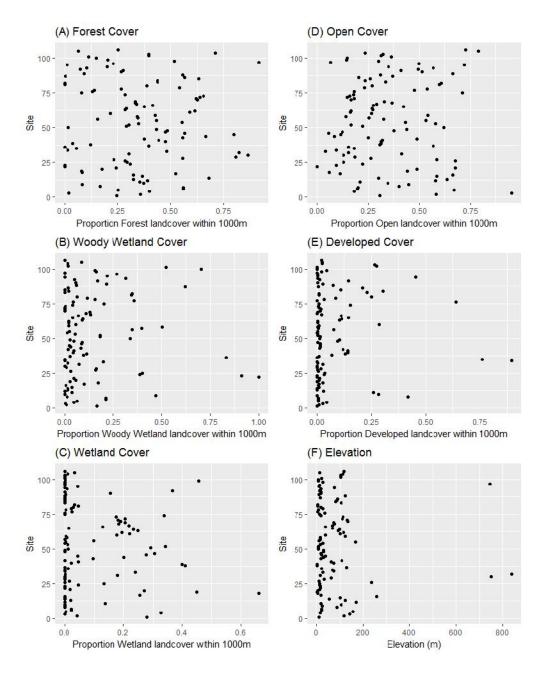


Figure 1.3: Proportion of surrounding land cover within 1000m for each land class grouping at all sites sampled. Forest cover (A) ranged from 2% to 92%; few sites had greater than 50% woody wetland (B) or wetland cover (C); cover of open area (D) varied greatly and was typically under 75% cover; sites ranged from no surrounding development (E) to moderate, with a few highly sites in highly developed areas; and most sites were at elevations below 300m (F), with the exception of three high altitude sites in Western Maryland.

1.3.2 Bee community overview

We collected from a total of 1139 weekly samples across the two years (813 in 2014 and 325 in 2015). Due to the varying level of detail to which volunteers recorded overturned cups and general reports that these events were infrequent, we did not attempt to correct for loss of the occasional cup trap. Therefore, we sampled a maximum of 10,251 individual cups across all sites and years, yielding an average of 1.2 bees per cup. The total number of bees collected was 12,510, representing 148 species, 21 genera and the following five families: Andrenidae, Halictidae, Apidae, Megachilidae and Colletidae. Approximately half of all bees collected species being *Andrena carlini* (2641 individuals) and *Andrena perplexa* (1079 individuals). The genera *Nomada* (15.4%), *Osmia* (14.1%), *Lasioglossum* (10.0%) and *Ceratina* (4.6%) were also prevalent in our samples. Of the 149 species collected, 25 were represented by a single individual and 17 had two individuals. 89 species were represented by at least 5 individual bees.

1.3.3 Ecological Guilds

Bees were grouped into ecological guilds based on their known or suspected nesting substrate, social structure and pollen diet breadth. A table of ecological information for all species collected can be found in Appendix B.1. The majority of bee species as a whole are solitary (Wcislo and Cane 1996), and this is reflected in our forest bees with more than three quarters of bees per site per year (n=143) having a solitary nesting behavior (Fig. 1.4A, x=66.27 \pm 6.14. Cleptoparasites were also fairly common (Fig. 1.4A, x=13.43 \pm 2.01). The majority of parasitic species were *Nomada* spp. (primarily parasites of *Andrena*, with some exceptions (Droege et al. 2010)), but

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also included *Sphecodes* spp. (primarily parasites of *Halictus* and *Lasioglossum* (Johansson et al. 1982)), *Lasioglossum platyparium* (parasitic in nests of other *Lasioglossum*), and the social parasite *Bombus citrinus*, whose hosts are other *Bombus* spp (Michener 2007).

The majority of bee species are ground nesting (Cane 1991), and the same was true for our samples with the overwhelming majority of bees surveyed per site per year soil nesting (x=64.97 \pm 6.73). The remaining bees were cavity nesting (x=12.27 \pm 1.41), nest in stem piths (x=4.01 \pm 1.03), nest in wood (x=2.42 \pm 0.23) or were social hive forming bees (x=1.47 \pm 0.29).

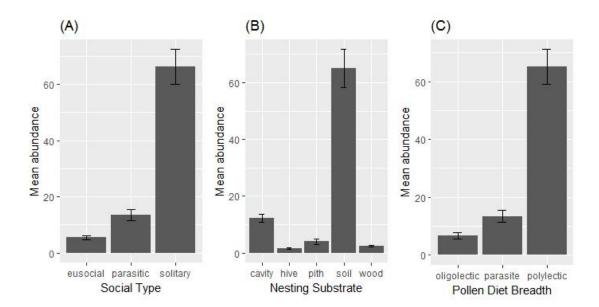


Figure 1.4: Mean abundance of bees per site and year by a) nesting substrate, b) social type and c) pollen diet breadth. The majority of bees collected were solitary, soil nesting and polylectic. (Error bars represent the standard error of the mean, n=143 site collections)

It is not surprising that most bees collected were polylectic (Fig. 1.4C, $x=65.04\pm 5.98$) as a generalist pollen diet is the predominant strategy across bee taxa. However, specialists comprised approximately 7% of the forest bee fauna (Fig. 1.4C, $x=6.66\pm1.17$), with 10 oligolectic species detected (Appendix B.1). Most of these specialist species were found in small numbers, although it is unclear whether they are truly uncommon or if this result is a sampling artifact. Presumably their more restricted search image when foraging could impact their likelihood to be drawn to bowl traps, or they may only be attracted to traps of a single color. Likewise, it is unclear whether bees foraging in the canopy, for example on Acer or Liriodendron, would be drawn down to bowl traps placed at ground level. Our most common specialist was Andrena erigeniae (n=782), which forages for pollen exclusively on the vernal woodland flower spring beauty (Claytonia). Andrena bradleyi, Andrena carolina, Colletes validus, Osmia virga and Habropoda laboriosa represent a group of species preferring ericaceous plants, especially Vaccinium and Rhododenron, and likely indicate acidic soils with ericaceous understories in the sites where they were found. The pollen diet of cleptoparasitic species ($x=13.43\pm2.01$) is, of course, the flowers visited by their nest host; however, for most species these relationships are unknown, and therefore we did not attempt to designate the parasitic species as oligolectic or polylectic (with the exception of *Bombus citrinus*).

1.3.4 Rare species and new records

Our survey produced a number of new county records and one new state record in Maryland, *Andrena rufosignata*, of which we collected 23 specimens in 7 different sites. The locations in which it was found range from the higher elevation western Maryland sites in Garret Co. to as far east as Harford Co., just north of Baltimore (Fig.

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1.5). Giles and Ascher (2006) previously suggested their survey in the Black Rock Forest Preserve as the southernmost range for *A.rufosignata*, but we now know it makes its way at least as far south as Montgomery CO.,MD (Fig. 1.5). *A. rufosignata* and a number of other species typically considered uncommon to rare in the region were surprisingly prevalent in our samples, indicating that these species may be closely tied to forests and have been previously under sampled due to a general focus on more open habitats. One of these potential woodland specialist bees *Andrena pruni* (n=303), despite previously being considered uncommon in the area (Droege, 2013), was our fifth most collected species, and is a member of the subgenus *Melandrena* with our most common species, *A.carlini*. Other uncommon *Andrena* spp. included *Andrena tridens*, which showed up in decent numbers in our woodlots (n=126), as well as *Andrena bradleyi* (n=3), and *Andrena hilaris* (n=4), which were not abundant in samples but were each detected in multiple sites and multiple counties.

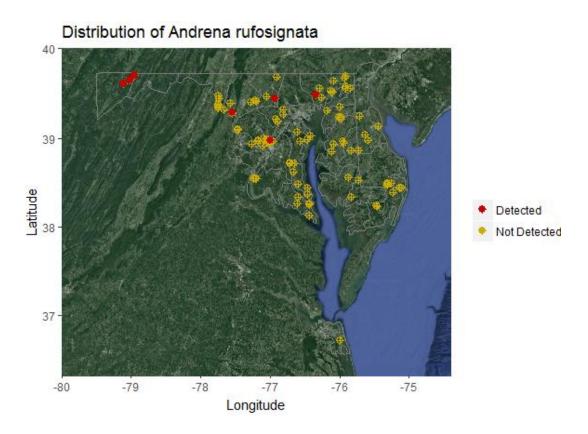


Figure 1.5: Distribution of *Andrena rufosignata* across both years, 2014 and 2015. Sites where *A. rufosignata* was captured in either 2014 or 2015 are in red, *A. rufosignata* was not captured in sites marked in yellow.

Among the *Lasioglossum* is a group of uncommon species in the subgenus *Dialictus* that appear to be associated with woodland habitats. These species include: *Lasioglossum coeruleum* (n=75), *Lasioglossum cressonii* (n=93) and *Lasioglossum subviridatum* (n=107), *Lasioglossum versans* (n=42), *Lasioglossum catellae* (n=14) as well as *Lasioglossum gotham* (212), a species that was first described by Gibbs in 2011. Several of these species were prominent in Droege's preliminary woodland survey (2013), and their high numbers in forested sites compared to more general surveys strongly suggests a place for them in the characteristic forest bee community.

1.3.5 Exotic species

Of the 148 species identified, 142 are native to North America and 6 are exotic. The mean number of native bees collected per site was 74.67 ± 7.2096 , with mean exotic bees equal to 10.46 ± 1.3178 (Fig. 1.6). The most prevalent introduced species were two congeners, Osmia taurus and Osmia cornifrons, both of which were introduced from Japan in 2000 and 1960, respectively (Russo, 2016). Both these species were widespread and abundant across the survey area, with Osmia taurus being the third most abundant bee species overall (n=1014). Of the total Osmia collected more than half were Osmia taurus (57.9%), and Osmia cornifrons (20.3%) were roughly as numerous as all native Osmia combined (21.5%). The native species belonging to the same subgenus of these two exotics, Osmia lignaria (Subgenus: *Osmia*) was scarce, with only 10 individuals captured across all sites and both years. Other introduced species include; the European honey bee, Apis mellifera (n=106), most common in sites sampled by bee keepers with nearby hives; Anthophora *plumipes* (n=13), another Japanese species introduced for crop pollination (Batra, 1994); and a single specimen each of two European species, Lasioglossum leucozonium and Andrena wilkella.

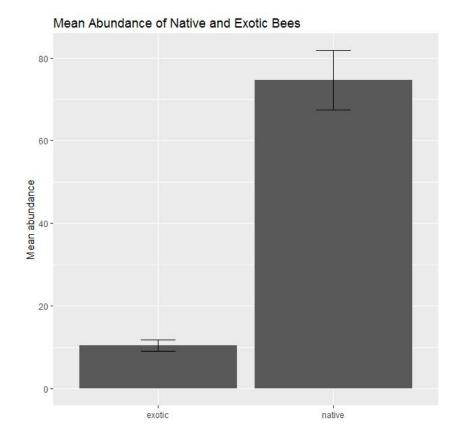


Figure 1.6: Mean abundance of native and exotic bees per site and year (Error bars represent the standard error of the mean, n=143 site collections). The majority of bees collected were native, although there were a few very prevalent exotic species.

It's difficult to say how exotic bee species might impact native species. The scarcity of the blue orchard bee, *O. lignaria*, compared to its exotic congeners is alarming, but declines in this species are difficult to document due to the lack of baseline data prior to introduction of *O. taurus* and *O. cornifrons*. However, anecdotal reports seem to suggest that the native species is much less common in our study region today than in the past (Sam Droege, pers. comm.).

1.3.6 Phenology

Forest bees are an ephemeral, vernal community, with activity beginning in early spring and dwindling by the time of canopy closure in early summer. Captures were low in the first few collection weeks of both years (Fig. 1.7) when mean temperatures across sites were below 50°F (Table 1.1). Abundance of bees increased in mid-April (Weeks 4-6) as temperatures reached the mid 50's. A drop in captures was seen in 2014 during week 5 (Fig. 1.7A), likely due to rain (Table 1.1, x males+females= $.74\pm0.08$ in.) and possibly wind (x males+females = 8.35 ± 0.21 mph.). A similar pattern was seen in 2015, with low captures in week 6 (Fig. 1.7B) during a period of high rainfall and wind (Table 1.1, although similar conditions during week 5 (Table 1.1) did not seem to impact bee captures (Fig. 1.7B). These differences could be due to the number of rainy days during the week more so than total rainfall.

Week	Start	2014 Weather Conditions			
		Mean Temp	Mean Precipitation	Mean Humidity	Mean Wind
Number	Date	(F)	(in)	(%)	(mph)
Week1	Mar. 14	42.58 ± 0.24	0.44 ± 0.08	61.42 ± 0.55	8.36 ± 0.23
Week2	Mar. 21	41.99 ± 0.30	0.82 ± 0.10	63.44 ± 0.60	7.86 ± 0.19
Week3	Mar. 28	50.58 ± 0.24	1.07 ± 0.10	71.15 ± 0.54	7.20 ± 0.19
Week4	Apr. 4	53.31 ± 0.26	0.37 ± 0.05	62.61 ± 0.63	6.86 ± 0.18
Week5	Apr. 11	55.03 ± 0.24	0.74 ± 0.08	61.34 ± 0.54	8.35 ± 0.21
Week6	Apr. 18	53.02 ± 0.22	0.55 ± 0.09	58.28 ± 0.68	6.90 ± 0.19
Week7	Apr. 25	57.71 ± 0.29	2.09 ± 0.22	68.50 ± 0.47	6.89 ± 0.19
Week8	May 2	62.08 ± 0.21	0.66 ± 0.12	65.46 ± 0.62	5.38 ± 0.16
Week9	May 9	66.61 ± 0.23	1.50 ± 0.15	72.98 ± 0.61	5.54 ± 0.15
Week10	May 16	65.15 ± 0.25	1.92 ± 0.20	68.79 ± 0.66	5.32 ± 0.15
Week11	May 23	65.82 ± 0.17	0.69 ± 0.07	67.97 ± 0.58	5.05 ± 0.16
Week12	May 30	68.26 ± 0.18	0.31 ± 0.03	66.82 ± 0.71	4.76 ± 0.17

Table 1.1:Weather conditions for each sample week, averaged across all sites
sampled.

Table 1.1 continued

Week	Start	2015 Weather Conditions			
Number	Date	Mean Temp (F)	Mean Precipitation (in)	Mean Humidity (%)	Mean Wind (mph)
Week1	Mar. 15	42.02 ± 0.39	0.30 ± 0.05	57.24 ± 0.79	6.33 ± 0.30
Week2	Mar. 22	45.31 ± 0.40	0.64 ± 0.12	56.98 ± 0.99	7.46 ± 0.30
Week3	Mar. 29	50.84 ± 0.53	0.22 ± 0.06	53.31 ± 0.89	8.98 ± 0.35
Week4	Apr. 5	53.32 ± 0.30	0.36 ± 0.07	69.01 ± 0.97	7.31 ± 0.35
Week5	Apr. 12	59.14 ± 0.43	0.88 ± 0.18	65.13 ± 0.95	6.43 ± 0.33
Week6	Apr. 19	54.49 ± 0.53	0.89 ± 0.17	56.69 ± 0.91	7.83 ± 0.29
Week7	Apr. 26	58.25 ± 0.52	0.18 ± 0.04	59.85 ± 0.84	5.74 ± 0.32
Week8	May 3	68.15 ± 0.42	0.51 ± 0.14	67.99 ± 0.86	5.16 ± 0.32
Week9	May 10	68.78 ± 0.40	0.61 ± 0.12	67.70 ± 0.77	6.00 ± 0.28
Week10	May 17	67.25 ± 0.40	0.73 ± 0.13	67.87 ± 0.74	6.11 ± 0.30
Week11	May 24	70.60 ± 0.42	1.02 ± 0.19	72.32 ± 0.70	7.04 ± 0.39
Week12	May 31	70.18 ± 0.35	1.45 ± 0.27	78.44 ± 0.74	7.09 ± 0.39

Maximum mean abundance in 2014 was during week 4 (Fig. 1.7A, x = males+females 17.96±2.33) and week 6 (Fig. 1.7A, $x males+females = 18.25\pm2.54$), and in 2015 was during week 5 (Fig. 1.7B, $x males+females = 23.38\pm3.87$). By late April (~week 7) in both years, capture rates had begun to decline, tapering off into May. By late May to early June most sites were collecting few or no bees (Fig. 1.7). In general, more males were captured than females, and abundance patterns for the sexes mirror one another (Fig. 1.7), although in 2015 fewer males than females were collected in weeks 6, 8 and 9 (Fig. 1.7B). Sex ratios in wild bees have not been well studied, and it is also unknown whether males and females are equally likely to be collected in pan traps. Males visit flowers for nectar and in some cases to located females, while females (except of cleptoparasitic species) collect both nectar and pollen. Therefore, visitation rates, foraging patterns and the likelihood of a bee approaching and entering a trap may differ by sex.

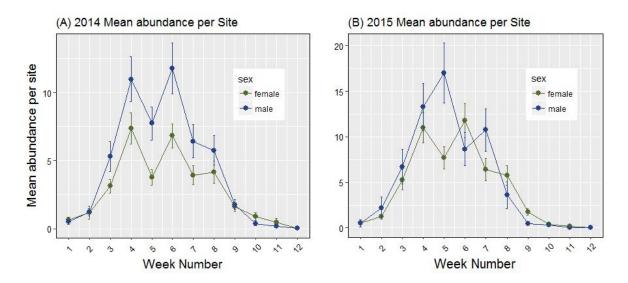


Figure 1.7: Phenology of all bee species represented as mean abundance per site per year in A) 2014 and B) 2015. Abundance peaked in mid-April both years, and few bees were collected after the start of May.

Individual species differ in their phenology, almost certainly in response to blooming period of their preferred host plants or overall availability of floral resources. This flight window may also be shaped by other factors, including a species' tolerance of unfavorable weather conditions, abundance of parasites or pathogens (or for cleptoparasitic species, phenology of the host), and competition with other floral visitors. Phenology of our most common species, *Andrena carlini*, mirrors that of the overall bee abundance, with mean abundance peaking around week 5 in both years, and quickly tapering off from week 7 (Fig. 1.8A,B). Interestingly, our second most common species, *Andrena perplexa*, appears to forage a few weeks later in the season, with numbers increasing in weeks 5 through 8 (Fig. 1.8C,D), just as *A. carlini* populations are declining. While both species are generalists, visiting a variety of flower species to meet their nutritional needs, it is likely that these phenological patterns reflect differences in the assemblage of woodland flowers used by each species. Given that both are very common woodland species of a similar size, it is also possible that competition between them has led to niche partitioning, but further investigation would be necessary to determine if and how the two species interact and impact one another.

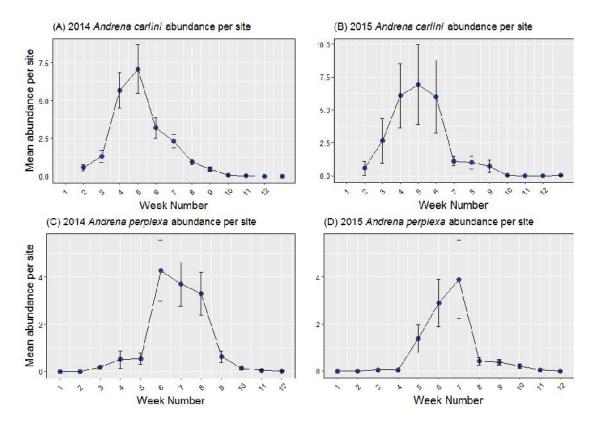


Figure 1.8: Mean abundance per site of *Andrena carlini* by sampling week in A) 2014 and B) 2015, and of *Andrena perplexa* in C) 2014 and D) 2015. *A. carlini* phenology was earlier than *A. perplexa* in both years.

Bees in the genus *Osmia* in general were most abundant through April (weeks 4-7, Fig. 1.9). Our two most common native *Osmia (O.pumila and O.atriventris)*,

were detected in low numbers throughout this window, especially in early April. Both exotic species were present throughout this time, although *O. taurus* numbers seem to peak sharply in first two weeks of April, while *O. cornifrons* is present in more steady numbers throughout the month (Fig. 1.9). If competition for floral or nesting resources exists between native and non-native *Osmia*, there does not appear to be enough phenological difference between the species to offer native *Osmia* a reprieve from spatial and temporal overlap with their exotic congeners. Differences in body size may protect *O. pumila* and *O. atriventris* to some degree from competition with the much larger exotic species. *O. lignaria* is similar in size to *O. taurus* and *O. cornifrons*, and may have a more similar pattern of resource use. This may explain why, of the native *Osmia*, we see the fewest records of *O. lignaria* in this now highly invaded region.

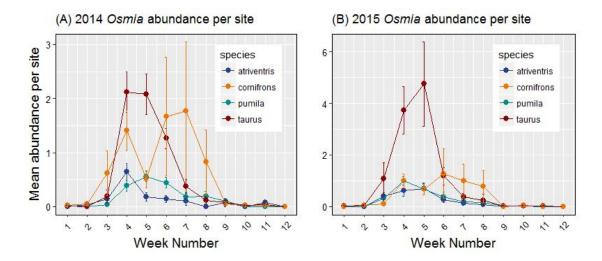


Figure 1.9: Mean abundance of *Osmia* spp. per site by sampling week in A) 2014 and B) 2015. The exotic species, *O. taurus* and *O. cornifrons*, were more abundant than native species.

1.3.7 Site level abundance, richness and species diversity

Sites varied greatly in bee abundance, species richness and diversity (a table of these metrics for all sites sampled can be found in Appendix A.1). Species abundance per site ranged from a single bee to 458 specimens, and the maximum species richness was 46 species at a single site and year (Appendix A.1). Abundance was generally low in the Coastal Plain, especially in the southern Delmarva peninsula, and highest in the piedmont and ridge areas of northern and western Maryland (Fig. 1.10). Patterns of species richness across the region were similar to abundance, with the most species rich sites in the piedmont and western Maryland and a general trend for low species richness in the coastal plains, especially along the Atlantic coast (Fig 1.11).

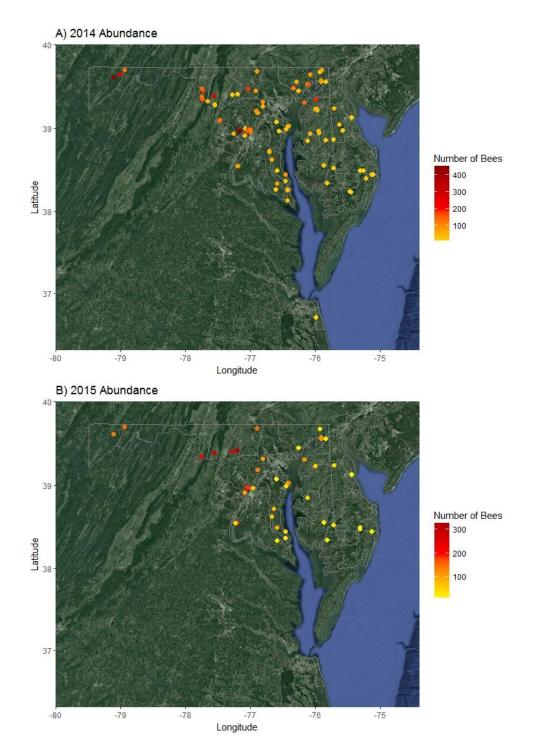


Figure 1.10: Sites sampled in A) 2014 and B) 2015, with site points colored by number of bees collected. Yellow indicates sites with the lowest abundance and red sites had the highest abundance.

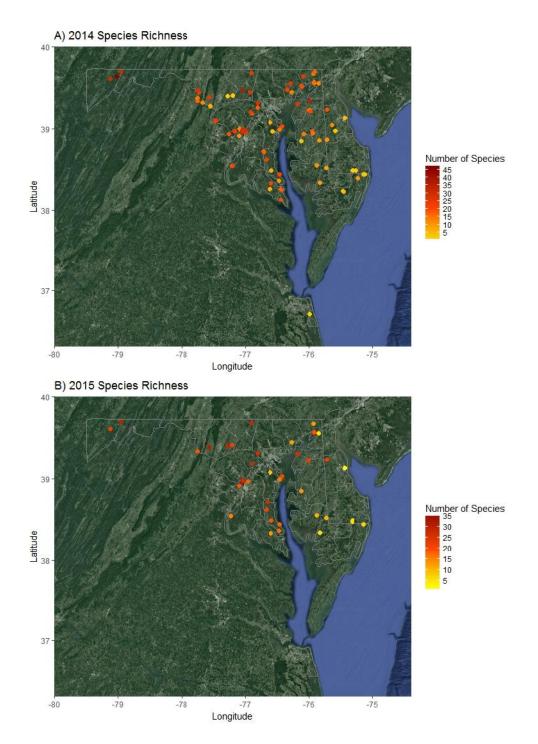


Figure 1.11: Sites sampled in A) 2014 and B) 2015, with site points colored by number of species. Yellow indicates sites with the lowest species richness and red sites had the greatest number of species.

The site with the greatest Shannon Diversity Index in 2014 (Site 97; H=3.05; Table 1.2), was one of our highest altitude sites, situated in the mixed hardwood watershed of Savage River State Forest, Garret Co. Maryland. Roughly a third of all species sampled in this study were found at this site, including 4 specimens of our new Maryland record, *A. rufosignata*. Though this state forest is intersected sporadically by agricultural fields, it is a relatively contiguous forest system. The numerous Savage River watersheds as well as a history of logging in the state forest may account for its ability to host a diverse suite of bees in an area with almost entirely forest cover.

Large forests surrounded by urban areas are also capable of supporting diverse pollinator populations, as evidenced by site 104, located near a suburban area in the Patapsco State Park outside Baltimore. Relatively few *Lasioglossum* were found at this site, with the few *Lasioglossum* spp. Droege (2013) postulated as woodland-associated absent. However, other species indicative of a forest community, including several species of both *Andrena* and *Nomada*, are present. The suburban landscape surrounding the forest may be responsible for the high diversity despite reduced abundance as compared to our Savage River site (Table 1.2). Another large urban forest patch, Rock Creek Park (site 86) in Washington D.C., had a diverse bee population (as did two other transects within RCP, sites 84 and 85; Appendix A.1).

2014 Sites with High Bee Diversity										
Site	Elev. (m)	Forest	Woody Wetl.	Open	Devel.	Wetl.	Abundance	Richness	Н	
Site 97	747	92%	0%	7%	0%	0%	253	46	3.05	
Site 104	115	71%	2%	24%	2%	1%	87	28	3.03	
Site 19	3	8%	3%	44%	0%	45%	44	23	2.98	
Site 90	19	27%	6%	51%	0%	15%	191	35	2.91	
Site 12	170	39%	0%	58%	3%	0%	80	26	2.89	
Site 42	110	37%	2%	49%	12%	0%	53	25	2.89	
Site 9	23	8%	47%	45%	0%	0%	34	19	2.82	
Site 86	89	57%	2%	21%	21%	0%	142	28	2.78	
Site 26	238	29%	3%	68%	1%	0%	183	36	2.75	
			2015	Sites wit	h High B	ee Divers	sity			
Site	Elev. (m)	Forest	Woody Wetl.	Open	Devel.	Wetl.	Abundance	Richness	Н	
Site 24	13	31%	39%	22%	3%	5%	73	23	2.93	
Site 19	3	8%	3%	44%	0%	45%	48	22	2.87	
Site 1	12	25%	17%	31%	0%	28%	111	26	2.86	
Site 104	115	71%	2%	24%	2%	1%	105	26	2.83	
Site 9	23	8%	47%	45%	0%	0%	37	22	2.81	

Table 1.2:Sites with the greatest Shannon diversity (H>2.75). Site coordinates can
be found in Appendix A.1.

Despite being surrounded by urban and suburban development, both sites 104 and 86 were in city parks large enough that the majority of land cover within 1000m of the transect was forest (Table 1.2), indicating that bee communities may be responding to landscape variables on a large scale, rather than the broader context. Small home ranges and high mobility may make many bee species better adapted to the constraints of highly fragmented habitat than vertebrates. Just how small and isolated a fragment can be and still have value as bee habitat requires further study, but our highly urban sites suggest that even small city patches have potential to support diverse populations. Fort Totten and Fort Slocum Parks in Washington D.C. are two small forest patches (17 and 6 hectares, respectively) in a sea of urban residential and commercial development. Within 1000m of the larger of the two parks, Fort Totten (Site 35), the landcover is 94% developed, yet species abundance, richness and diversity are medium to high relative to other sites surveyed (Table 1.3). Fort Slocum (Site 34) is smaller and had fewer bees and species (Table 1.3), but still a decent diversity that compared to many of our sites in more natural landscapes. Both communities were dominated by the widespread *A. carlini*, but also included some other woodland species such as *L. coeruleum* and *L. gotham*, with relatively few of the introduced *Osmia* spp.. While a closer look should be taken at bee distributions and dispersal in urban areas, these results are promising for conservation in highly developed and fragmented landscapes. City parks too small to accommodate most birds and mammals may still be able to increase habitat connectivity for bees, and likely other beneficial insects.

Table 1.3:Sites with high development within 1000m. Site coordinates can be
found in Appendix A.1.

Site ID	Elv	For.	Woody	Open	Devl.	Wetl.	Ab	un.	Ri	ch.	I	ł
	(m)		wet.				2014	2015	2014	2015	2014	2015
Site 34	74	1%	0%	9%	89%	0%	64	-	14	-	1.43	-
Site 35	69	6%	0%	18%	76%	0%	128	-	25	-	2.10	-
Site 76	15	13%	5%	18%	64%	0%	-	63	-	18	-	2.52
Site 94	75	20%	0%	35%	45%	0%	118	-	29	-	2.59	-
Site 8	86	17%	1%	40%	42%	0%	24	-	12	-	2.33	-

However, not every woodlot surveyed hosted an abundant and diverse community of bees, and sites in Eastern Shore MD and southern Delaware in particular were fairly depauperate. Two transects were sampled in Great Cypress Swamp Forest, a 10,000 acre parcel of mixed woody wetland in southern Delaware (Sites 23 and 36, Table 1.4). Very few bees inhabit this forest with sandy, water saturated soil. The few species we did find were primarily stem or wood nesting (eg. *Osmia* sp, *L. coeruleum*), indicating that soil conditions may explain the absence of our typical ground nesting community. Sites along the Atlantic coast (Sites 39 and 75) and the Chesapeake (Site 77) likewise had few bees (Table 1.4), and their communities were also characterized by a large proportion of stem nesting species.

Table 1.4:Sites with low abundance, richness and diversity. (Site coordinates can be
found in Appendix A.1)

Site ID	Elv	For.	Woody	Open	Devl.	Wetl.	Ab	un.	Ri	ch.	I	ł
	(m)		wet.				2014	2015	2014	2015	2014	2015
Site 39	3	4%	12%	31%	13%	40%	2	-	2	-	0.69	-
Site 75	36	8%	20%	71%	1%	0%	10	-	3	-	0.80	-
Site 77	7	14%	36%	48%	0%	2%	18	50	3	13	0.43	1.63
Site 23	18	0%	91%	9%	0%	0%	5	6	2	5	0.50	1.56
Site 36	21	0%	83%	15%	0%	1%	2	-	2	-	0.69	-

1.3.8 Comparing species composition among sites

To compare differences in species composition between sites we focused on sites sampled in both years to account for yearly fluctuations in populations and detection of species. Ordination based on abundance data showed sites fairly evenly distributed by ecological difference, with weak clustering (Fig. 1.12). Some of the observed differences between sites may be due to overall abundance at each site rather than true differences in species composition; several of the sites with the greatest distance from the center of the plot were those where very few bees were collected (eg. Sites 23, 50 and 56; Fig. 1.12). Likewise, very high abundance could set a site apart, as in site 30 which had our highest overall capture rate (n= 604). However, the presence of several species typical of only the northwestern part of the study area (according to Sam Droege, pers. com.; eg. *Bombus sandersoni, Lasioglossum acuminatum*) suggest that location in mountainous Garret Co. MD accounts for much of this difference. Similar to Site 30 in terms of Euclidean distance was another Garret Co. transect, Site 32 (Fig 1.12), which had fewer bees but a similar species composition including some northwestern species (eg. *Bombus vagans, Hylaeus annulatus*; range based on Sam Droege pers. com.).

The most distant site (Site 27) was a transect on Nature Conservancy land in Dorchester Co. MD. Seasonal flooding in this coastal plain forest limits tree growth and has resulted in a much more open canopy that most of the sites sampled. The species list reflects this with some open habitat associated species present (eg. *Agapostemon, Colletes inaequalis*), although our forest species are still represented (eg. A. *carlini, L.coeruleum*).

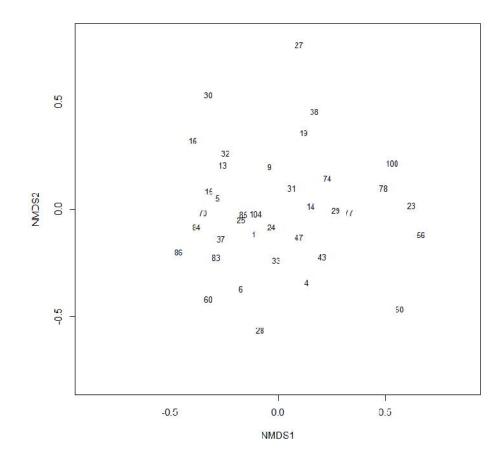


Figure 1.12: Non-metric multidimensional scaling plot of all sites sampled in both years using Hellinger transformed Euclidean distances on species level abundance data. 2014 and 2015 counts were summed for each site (dimensions=2; tries=20; stress=0.1058).

Chapter 2

WOODLAND BEE OCCUPANCY AND ABUNDANCE

2.1 Introduction

2.1.1 Background

Bees are the most important pollinators of both agricultural and natural systems, and understanding how they respond to landscape patterns has important economic and conservation implications. Land management for the promotion of pollinators depends on an understanding of the landscape variables driving bee occupancy and abundance. Despite the importance of these landscape effects on bee communities, few studies have addressed the impacts of land cover on bee communities.

Economic incentives for increasing wild bee pollination of crops have resulted in a number of studies looking at landscape effects on pollinator visitation to crops. Typically these studies have focused on farm management practices such as hedgerow plantings or preservation of natural patches around farms, and have sampled bees foraging in cultivated crops (Greenleaf and Kremen 2006; Carre et al. 2009; Julier and Roulston 2009; Le Feon et al. 2010; Kennedy et al. 2013; Morandin and Kremen 2013; Martins et al. 2015; Rollin et al 2015; Carrie et al. 2017). The general consensus is that increasing natural habitat surrounding agricultural fields increases bee abundance and diversity within crops, although responses to land cover types are not consistent across taxa and ecological groupings.

Landscape effects on bee communities have also been studied in urban settings with mixed results. Several studies spanning various geographical regions, habitat types and degrees of urbanization have documented loss of pollinator diversity and abundance in response to human development (McIntyre and Hostetler 2001; Cane et al. 2006; Taki 2007). However, a few studies have shown the opposite effect of urban development, finding bees to be most abundant and diverse in areas with moderate levels of disturbance (Winfree et al. 2007; Carper et al. 2014; Fortel et al. 2014). The conflicting results of such studies suggest that the effects of human development on bee communities vary regionally and are impacted by landscape context and differences in ecology of individual bee species (Kennedy et al. 2013). Because landscape effects on bee communities cannot be generalized across regions or habitat types, conservation and management decisions for pollinators on the landscape scale should be based on regional and habitat specific studies.

Landscape effects of bee communities in natural habitats rather than crop systems or urban settings are rarely studied (Taki et al. 2007; Winfree et al. 2007; Grundel et al 2010; Mandelik et al. 2012; Williams and Winfree 2013; Neame et al. 2013; Carper et al. 2014; Hopfenmuller et al. 2014), and many focus on *Bombus* spp (Jha and Kremen 2013), which can hardly be generalized to the small bodied, solitary species comprising the majority of bee fauna. Only a handful of such studies have been centered around temperate forest bee communities (Taki et al. 2007; Winfree et al. 2007; Williams and Winfree 2013; Carper et al 2014), and studies of bees in wooded habitats in general are uncommon.

Consequently, our knowledge of forest bee communities and forest pollination systems remains very limited. Many forest species are rarely encountered in cultivated crops, and so we know little about their ecology, distributions and population status, much less how land management might impact them on local and landscape scales. Conservation of natural areas is hinged on maintaining a robust population of bees capable of supporting native flowering plants through pollination services. The first step to ensuring preservation of this crucial ecosystem service is becoming familiar with the local pollinator fauna and investigating what drives their distributions and abundance.

To shed light on the landscape variables impacting woodland bees in the Mid-Atlantic region, we model occupancy and abundance of forest bee species using a variety of land cover classes. Individual bee species can vary in their habitat needs regarding diet breadth, nesting preferences and phenology; therefore, response to landscape structure tends not to be uniform across species (Kennedy et al. 2013). Rather than comparing community level variables or grouping species together, we present occupancy and abundance model results for a subset of species from our forested sites representing a range of taxa and ecological traits. Background on the six focal species is given in the following sections. We chose two species from our most common genus, Andrena; Andrena carlini is a common generalist, while A. erigeniae, also common, is oligolectic. These two species allow us to compare how closely related bees with different foraging pressures respond to landscape variables. From the Halictidae, we chose L. coeruleum, which also serves as a representative of species nesting in rotting wood rather than soil. Our most common Nomada species, N. *luteloides*, is presented to discuss patterns in distribution of cleptoparasites. Finally, we compare the exotic and now widespread Osmia taurus with a native congener, O. pumila.

2.1.1.1 Andrena carlini

A.carlini was the most commonly captured species in our survey and was detected in 84% of all sites sampled (Fig. 2.1). Like other species in the genus

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Andrena, A. carlini is solitary and females build subterranean nests where individual eggs are laid in cells with provisions of pollen and nectar. This large bodied *Andrena* species is polylectic, known to visit a wide variety of flowers (Schrader and LaBerge 1978), and is one of the primary pollinators of *Erythronium* spp (Banks 1980; Harder et al. 1985). *A.carlini* was the most common species in our survey and appears frequently in surveys of the eastern forest bee fauna (Giles et al 2006; Taki et al. 2007; Roberts et al. 2017).

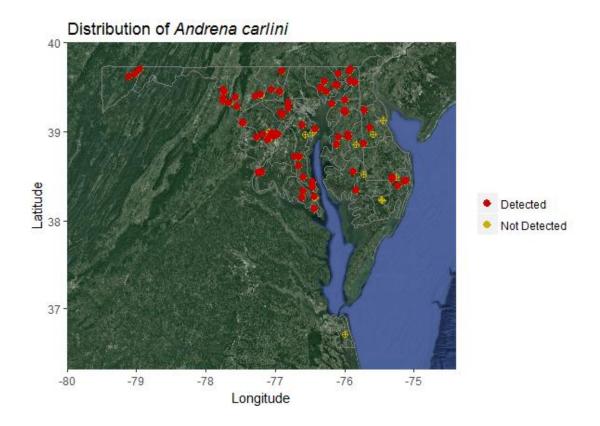


Figure 2.1: Distribution of *A. carlini*, a common woodland polylectic bee. Red points indicate sites where *A. carlini* was detected during the sampling period and yellow points are sites that were sampled and no *A. carlini* were detected.

2.1.1.2 Andrena erigeniae

Another ground nesting species common in eastern forests is the Spring Beauty bee, *A. erigeniae*, which collects pollen exclusively from *Claytonia virginica* (Davis and La Berge 1975). Although most oligolectic species had low abundance across our survey, *A. erigeniae* was one of the most prevalent species collected in more than half of sites sampled. However, it was not found in any sites in the southern Delmarva peninsula (Fig. 2.2), where it's host plant is also uncommon.

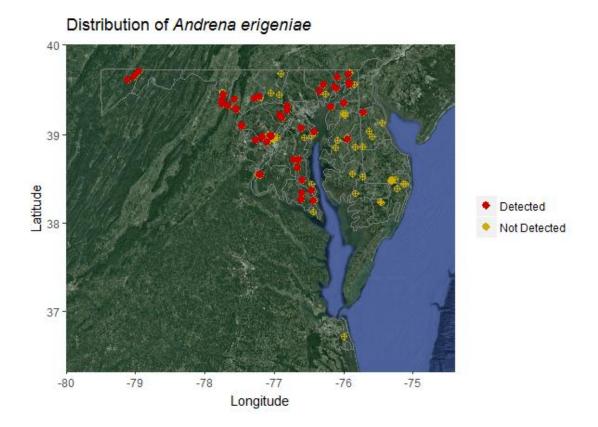


Figure 2.2: Distribution of *Andrena erigeniae*, the Spring Beauty bee. Red points indicate sites where *A. erigeniae* was detected during the sampling period and yellow points are sites that were sampled and no *A. erigeniae* were detected.

2.1.1.3 Lasioglossum coeruleum

The blue sweat bee, *L. coeruleum*, is a fairly uncommon polylectic bee generally associated with forest edges (Stockhammer 1967). Though many *Lasioglossum* spp. prefer open habitats, Droege (2013) suggested that a group within the genus, including *L. coeruleum*, may be more closely tied to forest. One of the few species in its family known to nest in wood, *L. coeruleum* prefers decaying branches and logs and is often found in elm and maple wood (Stockhammer 1967). This unusual nesting substrate compared to the majority of bee species that nest in soil (Cane 1992) may place unique selection pressures on *L. coeruleum* and other wood nesting species. It was surprisingly widespread and common in our survey, and inhabited many of the coastal plain sites not inhabited by *A. erigeniae* (Fig. 2.3).

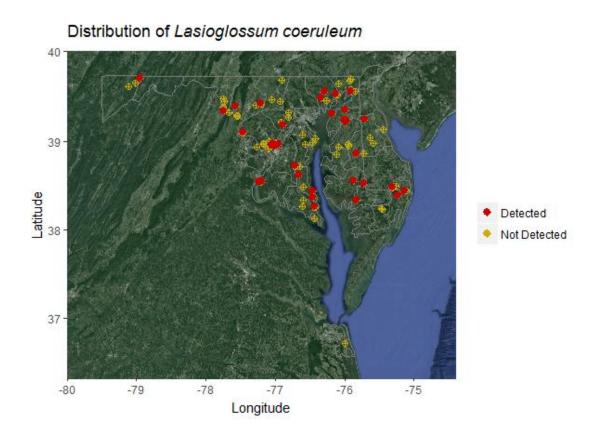


Figure 2.3: Distribution of the Blue Sweat bee, *L. coeruleum*. Red points indicate sites where *L.coeruleum* was detected during the sampling period and yellow points are sites that were sampled and no *L.coeruleum* were detected.

2.1.1.4 Nomada luteoloides

Bees in the genus *Nomada* are cleptoparasites, laying eggs in nests of hosts primarily in the genus *Andrena*, with some exceptions (Droege et al. 2010). The host of *N. luteoloides* has not been confirmed. Its high abundance and broad distribution across our survey area could indicate a relationship with one of our common widespread *Andrena*, and large body size makes the subgenus *Melandrena* (which includes *A.carlini*) a likely host group. Like *A. erigeniae*, it was not found in the most southern sites of the Delmarva (Fig. 2.4), but this is probably not suggestive of a direct relationship between the two species. The small body size of *A.erigeniae* makes it an unlikely host for *N. luteloides*.

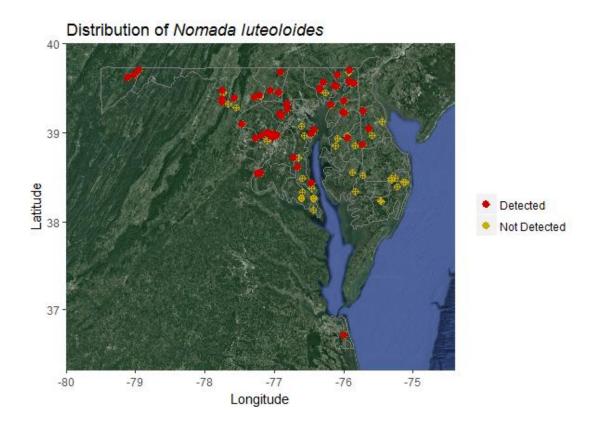


Figure 2.4: Distribution of the cleptoparasite *N. luteoloides*. Red points indicate sites where *N. luteoloides* was detected during the sampling period and yellow points are sites that were sampled and no *N. luteoloides* were detected.

2.1.1.5 Osmia taurus

Native to Japan, *O. taurus* was introduced accidentally to the eastern US in the 1990s or early 2000s (Biddinger et al. 2010). Both O. taurus and its relative *O. cornifrons* (introduced in 1977 for orchard pollination) are now well established

throughout the Mid-Atlantic, and the impacts they have on native *Osmia* are unknown. *O. cornifrons* is known to harbor common parasites with some North American *Osmia* species, but whether these parasites can be transmitted between species has yet to be confirmed (Russo 2016). *O. taurus* is polylectic and nests in pre-existing cavities in trees and logs. It was found in most sites surveyed and was our third most commonly collected bee (Fig. 2.5).

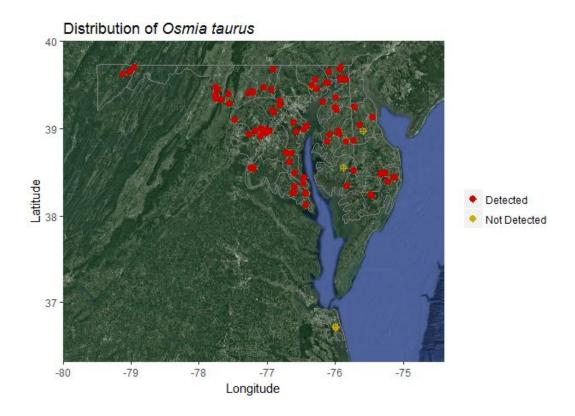


Figure 2.5: Distribution of the exotic orchard bee, *O. taurus*. Red points indicate sites where *O. taurus* was detected during the sampling period and yellow points are sites that were sampled and no *O. taurus* were detected.

2.1.1.6 Osmia pumila

O. pumila, belonging to the subgenus *Melanosmia*, is a smaller but ecologically similar species to *O. taurus* and *O. cornifrons* (subgenus *Osmia*), and was one of our most common and widespread native *Osmia* species (Fig. 2.6). (The only native member of the subgenus *Osmia*, to which our two introduced orchard bees belong, *O. lignaria*, was very uncommon (n=10), and therefore we did not attempt to model its occupancy and abundance.) Like *O. taurus*, *O. pumila* is a cavity nester and visits a broad range of floral hosts.

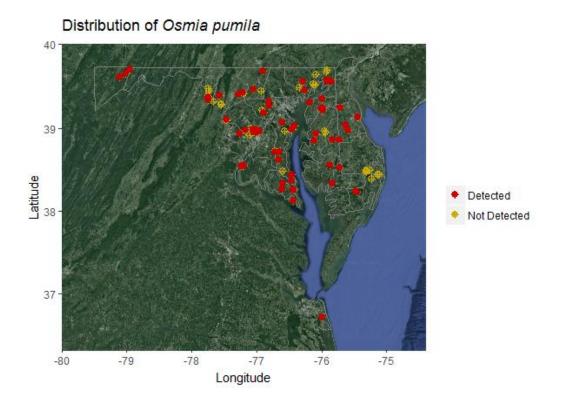


Figure 2.6: Distribution of the native *O. pumila*, a polylectic cavity nesting bee. Red points indicate sites where *O. pumila* was detected during the sampling period and yellow points are sites that were sampled and no *O.pumila* were detected.

2.1.2 Objectives

The primary objective of this study is to investigate how landscape variables impact the presence and abundance of bees in forests across gradients of urban development, natural and agricultural land covers and elevation. We present the results of occupancy and abundance modeling for six species to demonstrate varying responses to landscape variables by bees of different taxa and life histories.

2.2 Methods

Bee data, land cover variables and weather data were collected as described in Chapter 1. We analyzed bee data in the open-source statistical computing language R (Team R 2016) using the package "unmarked", which calculates single-season, singlespecies occupancy estimates, assuming a closed population. The function "occu" (Fiske et al. 2011) uses a hierarchical model design to account for variables that potentially affect detection probability using a Bernoulli distribution, and is shown in the nested design:

$$Z_i \sim \text{Bernoulli}()$$
 for $i = 1, 2, \dots, M$

where Zi is the unobserved occupancy state (i.e., present or absent) at site *i*, and i is the probability of occupancy at site *i*. This function of a Bernoulli distribution that describes site occupancy driven by species presence or absence at a given location is nested within the model for the detection process:

$$Y_{ij}|Zi \sim Bernoulli(Z_ip)$$
 for $j = 1, 2, ..., J_i$

where Y_{ij} is the estimated occupancy at site *i* and survey *j*, Z_i is the unobserved true occupancy state (from the function above), and p_{ij} is the detection probability at site *i* and survey *j* (MacKenzie et al. 2002, Royle and Dorazio 2008).

Hierarchical N-mixture species abundance models were also built in the "unmarked" package, using raw counts and the function "pcount" (Fiske et al. 2011), while also accounting for effects of observation-level covariates (weather and week number) on detection probability (Royle 2004) assuming a closed population. The model for true unobserved abundance is:

$$N_{it} \sim Poisson()$$
 for $i = 1, 2, \ldots, M$

where N_{it} is the true unobserved abundance at site *i* and time *t*, which is a function of the Poisson distribution, in which the mean is equal to the variance, with a mean of at site *i* at time *t*. This model is nested within the model describing the detection process:

$$Y_{iit}|N_{it} \sim Binomial (N_{it}, p_{ijt})$$

where Y_{ijt} is the observed abundance at site *i* during visit *j* at time *t*, which is a function of a binomial random variable with the parameters N_{it} (true abundance at site *i* at time *t* and p_{ijt} (detection probability at site *i* during visit *j* at time *t*) (Royle 2004, Kéry et al. 2005).

Detection probability was modeled based on the detection covariates average temperature, average humidity, average windspeed and weekly precipitation as well as week number. Models containing each of these variables, a null model and a global model containing all detection covariates were compared using Akaike's information criterion (AIC; Akaike 1981). The two best fit models (temperature and week number) were used as detection covariates in all landscape models.

Models were developed to test for relationships between land cover variables and species occupancy and abundance, and model comparison for both occupancy and abundance models was based on AIC. Models meeting the criterion deltaAIC<2 were used to estimate predicted occupancy and abundance values and plotted.

2.3 Results and Discussion

Bee species can differ greatly in their ecological requirements and response to variables at the landscape scale. Rather than lose valuable information on how landscape impacts bee occupancy and abundance by modeling these patterns for groupings of species, we present model results for a select group of representative species showing a diverse possible range of responses to land cover. The six focal species are discussed in the sections below.

2.3.1 Andrena carlini Occupancy and Abundance

A common and widespread species that was found in most of the sites we sampled, *Andrena carlini* seems to be suited to forest habitats across a wide range of land cover gradients. Comparison of occupancy models for *A. carlini* showed the proportion of wetland land cover within a 200m buffer around the transect to be the best fitting model of those tested (Table 2.1). The two next best fit models- wetland cover within 500m and elevation in meters- did not meet our selection criteria of deltaAIC<2.0 (Table 2.1).

Table 2.1:Model selection results for A. carlini occupancy models, ranked by
deltaAIC. Only one model, wetland within 200m buffer, met the
selection criterion of deltaAIC<2. Detection covariates temperature and
week number were included in all models.

model	nPars	AIC	delta	AICwt	cumltvWt
wetland200	5	2702.8054	0.0000	0.9158	0.9158
wetland500	5	2708.8641	6.0587	0.0443	0.9600
elevation	5	2711.7710	8.9656	0.0103	0.9704
wetland1000	5	2712.3374	9.5320	0.0078	0.9782
null	4	2714.2338	11.4285	0.0030	0.9812
open1000	5	2714.8026	11.9972	0.0023	0.9835
developed500	5	2715.2729	12.4676	0.0018	0.9853
woodywetland500	5	2715.4902	12.6849	0.0016	0.9869
forest1000	5	2715.6075	12.8021	0.0015	0.9884
open500	5	2715.6577	12.8524	0.0015	0.9899
woodywetland1000	5	2715.7783	12.9729	0.0014	0.9913
forest500	5	2715.8031	12.9977	0.0014	0.9927
developed200	5	2715.8742	13.0688	0.0013	0.9940
open200	5	2716.0077	13.2024	0.0012	0.9952
developed1000	5	2716.0078	13.2025	0.0012	0.9965
year	5	2716.1013	13.2960	0.0012	0.9977
woodywetland200	5	2716.1292	13.3238	0.0012	0.9988

Predicted probability of occurrence is positively associated with wetland cover within 200m (Fig. 2.7A; $= 12.2 \pm 5.5$, p=0.03), particularly when wetlands comprise 20% or less of the land cover within 200m. Woody wetland cover, on the other hand, was not among our top ranked models (Table 2.1). Infiltration of wetlands and open water into forested areas likely promotes the type of open canopy forest preferred by many bee species (presumably by molding the community of flowering plants), while still providing suitable soil conditions for ground nesting species in drier areas and along creek banks. Upland sites may also be more likely to have a history of use as farmland than low, wet woodlands. Therefore, it's possible that wetland cover is an indirect indicator of forest age, and it is forest tenure, rather than wetland land cover, that *A. carlini* populations respond to.

While they did not meet our model selection criteria, wetland cover within 500 meters (Fig. 2.7B; $= 3.9\pm1.7$, p=0.02) and elevation (Fig. 2.7C; $= -0.002\pm0.001$, p=0.04) were both significant predictors of *A. carlini* occupancy. Like wetlands on a smaller scale, wetland within 500m was positively associated with occupancy, and - coefficient estimates did not overlap with zero. Therefore, wetland within 500m of a sampling site does seem to have biological significance, despite the model having a weak fit relative to other models, reinforcing the notion that *A. carlini* prefers bottomland forests with some penetration of wetlands. The same is true for elevation, which also had a weak model fit based on deltaAIC, but had a significant negative relationship with probability of occupancy. While slope estimates () are small, they do not overlap with zero, indicating a biologically important trend of decreasing probability of *A. carlini* with increasing elevation.

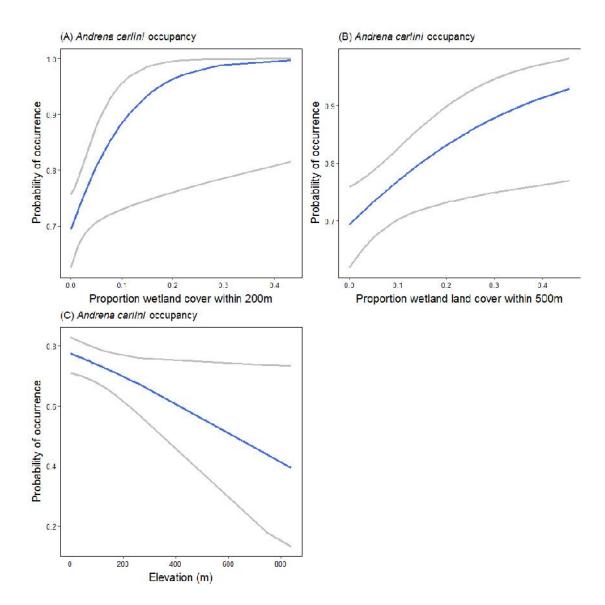


Figure 2.7: Predicted probability of *A. carlini* occurrence and SE based on the best fit occupancy models. Only the model including wetland within a 200m buffer (A; = 3.9 ± 1.7 , *p*=0.02) met our selection criterion of deltaAIC<2. Wetland within 500m (B; = 3.9 ± 1.7 , *p*=0.02) and elevation (C; = -0.002 ± 0.001 , *p*=0.04) did not meet selection criteria, but both occupancy models were significant at p<0.05 and slope estimates did not overlap with zero.

Of the abundance models tested, the global model containing all covariates was the best fit and the only model to meet the selection criterion (Table 2.2). This suggests that either our land cover variables are not good predictors of abundance for this species, or that abundance depends on a complex combination of habitat variables.

Table 2.2:	Model selection results for A. carlini abundance models, ranked by
	deltaAIC. Only the global model met the selection criterion of
	deltaAIC<2. Detection covariates temperature and week number were
	included in all models.

model	nPars	AIC	delta	AICwt	cumltvWt
global	21	11299.7444	0.0000	1.0000	1.0000
elevation	5	11752.9983	453.2539	0.0000	1.0000
developed500	5	11800.3639	500.6195	0.0000	1.0000
developed1000	5	11813.2448	513.5004	0.0000	1.0000
woodywetland1000	5	11824.7714	525.0270	0.0000	1.0000
woodywetland500	5	11847.2471	547.5026	0.0000	1.0000
developed200	5	11851.0306	551.2862	0.0000	1.0000
forest200	5	11851.8390	552.0946	0.0000	1.0000
open200	5	11856.9032	557.1588	0.0000	1.0000
wetland200	5	11871.1669	571.4225	0.0000	1.0000
forest1000	5	11871.5964	571.8520	0.0000	1.0000
forest500	5	11874.8695	575.1251	0.0000	1.0000
woodywetland200	5	11894.0498	594.3054	0.0000	1.0000
year	5	11901.6988	601.9544	0.0000	1.0000
wetland1000	5	11902.7736	603.0292	0.0000	1.0000
open500	5	11904.3707	604.6263	0.0000	1.0000
wetland500	5	11905.7275	605.9831	0.0000	1.0000
null	4	11905.8108	606.0663	0.0000	1.0000
open1000	5	11906.1281	606.3837	0.0000	1.0000

However, our next two best fitting models, elevation (Fig. 2.8A; = - 0.005 ± 0.0005 , p<0.05) and developed land cover within 500m buffer (Fig 2.8B; = - 3.22 ± 0.40 , p<0.05), both had a significant negative relationship with abundance and non-zero slope estimates. The association between *A. carlini* abundance and

elevation, again, may be tied to a preference for bottomland woodlands, but could also be due to differences in plant communities at varying elevations. Increased impervious surface reducing potential nesting area could explain decreased abundance with increasing developed land cover, but further investigation would be necessary to definitively explain these relationships.

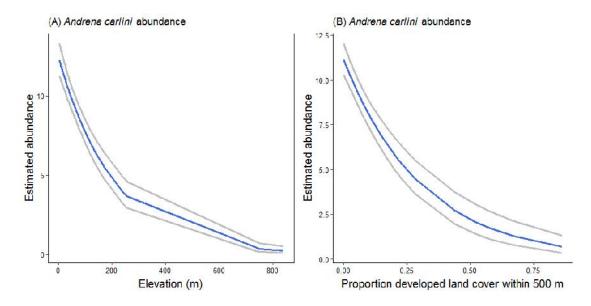


Figure 2.8: Predicted abundance of *A. carlini* and SE based on the best fit abundance models. Only the global abundance model fit our selections criterion of detlaAIC<2. The next two best fitting models, elevation (A; = -0.005 ± 0.0005 , *p*<0.05) and developed land cover within a 1000m buffer (B; = -3.22 ± 0.40 , *p*<0.05), did not meet the selection criterion but were significant at *p*<0.05 and slope estimates did not overlap zero.

2.3.2 Andrena erigeniae Occupancy and Abundance

Occupancy model results for our oligolectic *Andrena* were similar to the generalist *A. carlini*, with the two best fit models being wetland cover within 200m and 500m (Table 2.3).

Table 2.3:Model selection results for A. erigeniae occupancy models, ranked by
deltaAIC. Models of wetland landcover within 200m and 500m met the
selection criterion of deltaAIC<2. Detection covariates temperature and
week number were included in all models.

model	nPars	AIC	delta	AICwt	cumltvWt
wetland200	5	1606.3537	0.0000	0.2403	0.2403
wetland500	5	1607.3344	0.9807	0.1472	0.3875
wetland1000	5	1608.5227	2.1690	0.0812	0.4687
null	4	1609.0051	2.6514	0.0638	0.5325
year	5	1609.2056	2.8519	0.0577	0.5903
open1000	5	1609.3384	2.9847	0.0540	0.6443
woodywetland1000	5	1609.6038	3.2501	0.0473	0.6916
forest1000	5	1610.1501	3.7964	0.0360	0.7276
open500	5	1610.4039	4.0502	0.0317	0.7593
elevation	5	1610.5124	4.1587	0.0300	0.7894
woodywetland500	5	1610.5783	4.2247	0.0291	0.8184
woodywetland200	5	1610.7399	4.3862	0.0268	0.8452
developed1000	5	1610.7602	4.4066	0.0265	0.8718
forest500	5	1610.7700	4.4163	0.0264	0.8982
open200	5	1610.7752	4.4215	0.0263	0.9245
forest200	5	1610.8461	4.4925	0.0254	0.9500
developed500	5	1610.8842	4.5305	0.0249	0.9749
developed200	5	1610.9821	4.6285	0.0238	0.9987
global	21	1616.7222	10.3685	0.0013	1.0000

Neither of these models significantly predicted *A. erigeniae* occupancy, but the trend for both was an increasing probability of *A. erigeniae* occupancy with increasing wetland cover (Fig. 2.9). Slope estimates greater than zero for both wetland within 200m ($=4.36\pm2.30$) and 500m ($=2.12\pm1.13$) may indicate a biologically important, though not statistically significant, relationship between *A. erigeniae* occupancy and wetland cover on these scales. This relationship is likely complicated by factors impacting the distribution and abundance of *A. erigeniae*'s floral host, *Claytonia virginica*.

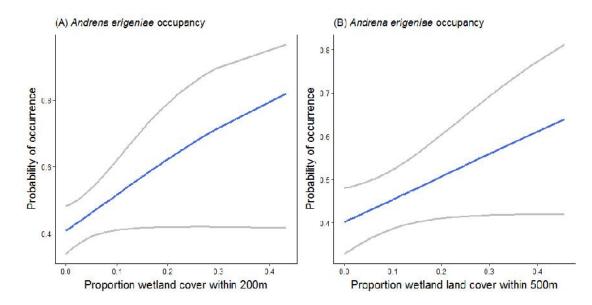


Figure 2.9: Predicted occupancy of *A. erigeniae* and SE based on the best fit occupancy models. Models of wetland land cover within 200m (A; $= 4.36\pm2.30, p=0.06$) and 500m (B; $= 2.12\pm1.13, p=0.06$) met the selection criterion of deltaAIC<2 and slope estimates did not overlap zero, but neither were significant at p<0.05.

The only model meeting the selection criterion for *A.erigeniae* abundance was the global model (Table 2.4). The next best fit models were wetland land cover within 500m and open land cover within 500m.

Table 2.4:Model selection results for A. erigeniae abundance models, ranked by
deltaAIC. Only the global model met the selection criterion of
deltaAIC<2. Detection covariates temperature and week number were
included in all models.

model	nPars	AIC	delta	AICwt	cumltvWt
global	21	4750.9035	0.0000	1.0000	1.0000
wetland500	5	4921.9824	171.0788	0.0000	1.0000
open500	5	4925.8558	174.9523	0.0000	1.0000
open200	5	4964.5355	213.6319	0.0000	1.0000
wetland200	5	4967.2322	216.3287	0.0000	1.0000

Table 2.4 continued

open1000	5	4973.1578	222.2543	0.0000	1.0000
elevation	5	4979.5859	228.6824	0.0000	1.0000
wetland1000	5	4985.2661	234.3626	0.0000	1.0000
woodywetland200	5	4990.3244	239.4209	0.0000	1.0000
year	5	4992.9690	242.0655	0.0000	1.0000
developed200	5	4995.2609	244.3573	0.0000	1.0000
forest200	5	4996.6338	245.7303	0.0000	1.0000
woodywetland500	5	4996.6751	245.7716	0.0000	1.0000
developed1000	5	4997.5461	246.6425	0.0000	1.0000
null	4	4997.8425	246.9390	0.0000	1.0000
forest1000	5	4998.7754	247.8718	0.0000	1.0000
developed500	5	4999.3832	248.4797	0.0000	1.0000
forest500	5	4999.6690	248.7654	0.0000	1.0000
woodywetland1000	5	4999.8424	248.9388	0.0000	1.0000

Although neither met the selection criterion, both best fit models after the global model did significantly predict *A. erigeniae* abundance (Fig. 2.10). Abundance increased with increasing wetland land cover within 500m (Fig. 2.10A; = 2.84 ± 0.30 , p<0.05). Given that *A. erigeniae* and its host plant (*Claytonia*) are both common and widespread, we are not surprised to see occupancy patterns reflecting those of *A. carlini*. Both species seem to prefer bottomland woodlands where low wet areas presumably create enough canopy gaps to support flowering forbs, including *Claytonia*. If these wetland-infiltrated areas are associated with older woodlands, it may be that more mature forests have better established communities of flowering plants, like *Claytonia*. However, cover of open land seems to have more bearing on *A. erigeniae*, with increasing open land cover within 500m decreasing predicted abundance (Fig. 2.10B; = 2.24 ± 0.27 , p<0.05). While *Claytonia* can be found flowering just beyond the edge of forests, it rarely ventures out into open fields or

crops. These open areas do not serve as alternative foraging areas for this specialist species, as they might for polylectic bees.

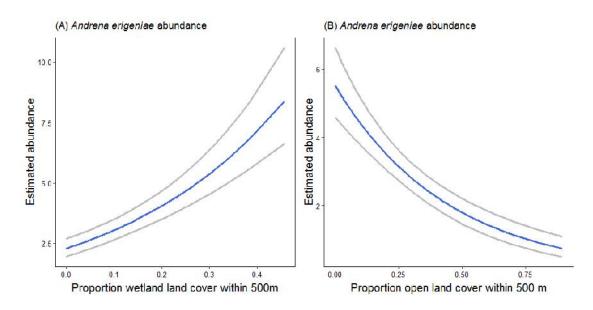


Figure 2.10: Predicted abundance of *A. erigeniae* and SE based on the best fit abundance models. Neither model met the selection criterion deltaAIC<2, but both wetland land cover within 500m (A; = 2.84 ± 0.30 , p<0.05) and open land cover within 500m (B; = 2.24 ± 0.27 , p<0.0) were significant at p<0.05 and had slope estimates that do not overlap 0.

2.3.3 Lasioglossum coeruleum Occupancy and Abundance

As discussed in Chapter 1, we believe *L. coeruleum* is closely tied to forest habitats given its high abundance in our samples compared to surveys of nearby open areas. Occupancy model comparison found the best fitting models to be woody wetland cover within buffers of 1000m and 500m (Table 2.5).

Table 2.5:Model selection results for *L. coeruleum* occupancy models, ranked by
deltaAIC. Models including the covariates woody wetland cover within
1000m and 500m met the selection criterion of deltaAIC<2. Detection
covariates temperature and week number were included in all models.

model	nPars	AIC	delta	AICwt	cumltvWt
woodywetland1000	5	550.7524	0.0000	0.3617	0.3617
woodywetland500	5	551.8509	1.0985	0.2088	0.5705
woodywetland200	5	554.2410	3.4886	0.0632	0.6337
wetland1000	5	554.5619	3.8095	0.0538	0.6875
forest500	5	554.5876	3.8352	0.0531	0.7407
forest1000	5	555.5552	4.8028	0.0328	0.7734
wetland500	5	555.8069	5.0545	0.0289	0.8023
forest200	5	555.8552	5.1028	0.0282	0.8305
null	4	556.2897	5.5373	0.0227	0.8532
global	22	556.4865	5.7341	0.0206	0.8738
wetland200	5	556.7037	5.9513	0.0184	0.8922
developed1000	5	556.8646	6.1122	0.0170	0.9093
open1000	5	556.9928	6.2405	0.0160	0.9252
developed500	5	557.2284	6.4760	0.0142	0.9394
year	5	557.5784	6.8260	0.0119	0.9513
elevation	5	557.7192	6.9669	0.0111	0.9624
open500	5	557.7706	7.0182	0.0108	0.9733

Positive relationships between occupancy and woody wetland cover were not significant at either scale (Fig. 2.11), but -coefficient estimates in both models are positive and do not overlap with 0, suggesting a trend for increased likelihood of *L*. *coeruleum* occupancy with increasing woody wetland cover. Therefore, despite lack of statistical significance, woody wetland may be biologically significant to occupancy for *L. coeruleum*.

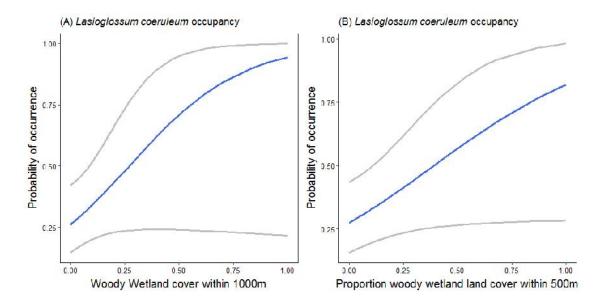


Figure 2.11: Predicted probability of *L. coeruleum* occurrence and SE based on the best fit occupancy models. The models including woody wetland within a 1000m buffer (A; p=0.08, $\beta=3.85\pm2.17$) and within 500m (B; p=0.05; $\beta=2.48\pm1.28$) met our selection criterion of deltaAIC<2, but neither was significant at p<0.05.

Abundance modeling resulted in many models fitting our selection criterion, with the best fit models being forest land cover within 500m, woody wetland within 1000m and woody wetland within 500m (Table 2.6).

Table 2.6:Model selection results for *L. coeruleum* abundance models, ranked by
deltaAIC. Models including the covariates forest cover within 500m and
1000m, woody wetland cover at all scales and wetland within 1000m met
the selection criterion of deltaAIC<2. Detection covariates temperature
and week number were included in all models.

model	nPars	AIC	delta	AICwt	cumltvWt
forest500	5	665.2556	0.0000	0.1629	0.1629
woodywetland1000	5	665.5762	0.3205	0.1388	0.3017
woodywetland500	5	665.5881	0.3325	0.1380	0.4396
woodywetland200	5	666.0486	0.7930	0.1096	0.5492

Table 2.6 continued

wetland1000	5	666.0504	0.7947	0.1095	0.6587
forest1000	5	666.7848	1.5292	0.0758	0.7345
wetland200	5	667.3140	2.0584	0.0582	0.7928
forest200	5	667.8136	2.5580	0.0453	0.8381
year	5	668.5678	3.3122	0.0311	0.8692
wetland500	5	668.8513	3.5957	0.0270	0.8962
open1000	5	669.2784	4.0228	0.0218	0.9180
null	4	669.3276	4.0719	0.0213	0.9392
open500	5	670.0770	4.8213	0.0146	0.9539
elevation	5	670.2954	5.0397	0.0131	0.9670
developed500	5	671.1773	5.9216	0.0084	0.9754
developed200	5	671.1882	5.9326	0.0084	0.9838
developed1000	5	671.2335	5.9778	0.0082	0.9920
open200	5	671.2866	6.0310	0.0080	1.0000
global	21	683.4862	18.2306	0.0000	1.0000

Abundance was negatively associated with increasing forest land cover, within 500m (Fig. 2.12A; β = -1.308±0.540, *p*=0.02). These results suggest that *L. coeruleum* is not associated with large extensive forest, but does not eliminate the possibility of it as a forest associated bee. Because our study looks only at forested sites, our data compare only different types of wooded habitats and not bee distributions across more general habitat types; therefore, our models address the influence of forest size (as addressed by surrounding forest land cover) and surrounding land cover but not how likely a species is to occupy forested sites. Therefore, it is still possible that *L. coeruleum* is closely associated with forest, but prefers smaller forest patches or forest edge to extensive forest.

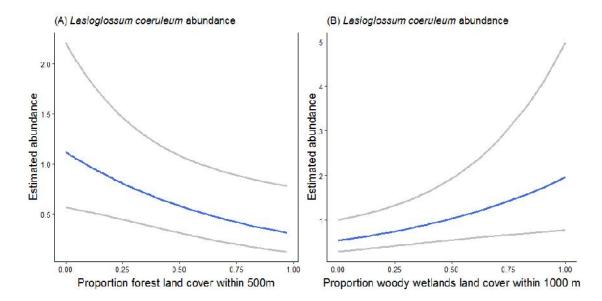


Figure 2.12: Predicted abundance of *L. coeruleum* and SE based on the best fit abundance models. The models including forest land cover within 500m (A) and woody wetland land cover within 1000m (B) both met our selection criterion of detlaAIC<2 and were significant at p<0.05.

While the occupancy models with woody wetlands were not statistically significant, woody wetland cover within 1000m positively predicts *L. coeruleum* abundance (Fig. 2.12B; β = 1.28±0.49, *p*=0.01). Most of the sites with significant cover of woody wetlands were on the Delmarva peninsula, an area that in general had low abundance and species richness. We suspect this trend is in part due to either soil composition or saturation restricting suitable nesting sites for many ground nesting species. *L. coeruleum* nests in rotting wood, and therefore would be less impacted by soil characteristics. However, the community of plants occupying these low woodlands and the foraging preferences of different bee species is likely also important in shaping the pollinator community.

2.3.4 Nomada luteoloides Occupancy and Abundance

All occupancy models except the global model met the selection criterion for *N. luteoloides*, and the best fit model was the null model (Table 2.7). When predictions based on the next best fit models were plotted, none were significant. Most likely, landscape variables only indirectly impact occupancy of cleptoparasites by shaping the distribution of potential hosts. Because the nest host(s) of *N. luteoloides* have not been confirmed, we are not able to make occupancy predictions based on host occupancy.

Table 2.7:Model selection results for *N. luteoloides* occupancy models, ranked by
deltaAIC. All models tested except the global model met the selection
criterion of deltaAIC<2. Detection covariates temperature and week
number were included in all models.

model	nPars	AIC	delta	AICwt	cumltvWt
null	4	1572.1963	0.0000	0.1190	0.1190
developed200	5	1573.2002	1.0039	0.0720	0.1910
wetland1000	5	1573.2462	1.0499	0.0704	0.2613
elevation	5	1573.5620	1.3657	0.0601	0.3214
forest500	5	1573.6578	1.4616	0.0573	0.3787
developed500	5	1573.6862	1.4899	0.0565	0.4352
woodywetland500	5	1573.6919	1.4956	0.0563	0.4915
woodywetland1000	5	1573.8276	1.6314	0.0526	0.5441
wetland500	5	1573.9974	1.8012	0.0483	0.5924
open1000	5	1574.0110	1.8148	0.0480	0.6404
year	5	1574.0150	1.8188	0.0479	0.6884
woodywetland200	5	1574.1047	1.9084	0.0458	0.7342
open500	5	1574.1455	1.9493	0.0449	0.7791
forest1000	5	1574.1614	1.9651	0.0445	0.8236
developed1000	5	1574.1629	1.9667	0.0445	0.8681
open200	5	1574.1740	1.9777	0.0443	0.9123
forest200	5	1574.1906	1.9944	0.0439	0.9562
wetland200	5	1574.1961	1.9998	0.0438	1.0000
global	21	1589.5247	17.3284	0.0000	1.0000

The best fit model for *N. luteoloides* abundance was the global model (Table 2.8), again suggesting that none of the landscape variables tested were particularly relevant to predicting abundance.

Table 2.8:Model selection results for *N. luteoloides* abundance models, ranked by
deltaAIC. Only the global model met the selection criterion of
deltaAIC<2. Detection covariates temperature and week number were
included in all models.

model	nPars	AIC	delta	AICwt	cumltvWt
global	21	3380.2849	0.0000	1.0000	1.0000
woodywetland500	5	3480.0831	99.7983	0.0000	1.0000
wetland200	5	3485.4811	105.1962	0.0000	1.0000
wetland1000	5	3488.5493	108.2644	0.0000	1.0000
woodywetland1000	5	3489.5773	109.2924	0.0000	1.0000
forest500	5	3489.7293	109.4444	0.0000	1.0000
forest1000	5	3492.1803	111.8954	0.0000	1.0000
woodywetland200	5	3493.7011	113.4162	0.0000	1.0000
wetland500	5	3497.1512	116.8663	0.0000	1.0000
developed1000	5	3499.2220	118.9371	0.0000	1.0000
forest200	5	3501.2036	120.9187	0.0000	1.0000
elevation	5	3501.7011	121.4162	0.0000	1.0000
year	5	3502.7841	122.4992	0.0000	1.0000
null	4	3504.0080	123.7231	0.0000	1.0000
developed500	5	3505.1310	124.8461	0.0000	1.0000
developed200	5	3505.3474	125.0625	0.0000	1.0000
open1000	5	3505.5949	125.3100	0.0000	1.0000
open500	5	3505.8291	125.5442	0.0000	1.0000
open200	5	3506.0073	125.7224	0.0000	1.0000

However, the two next best fit models, despite not meeting the model selection criterion, were significant. Woody wetlands within 500m had a positive relationship with *N. luteoloides* abundance (Fig. 2.13A; p<.05), similar to some of the other species covered here. However, wetland land cover within 200m was negatively

associated with *N. luteoloides* abundance (Fig. 2.13B; p<0.05). Given that occupancy probability of the likely host species, *A. carlini*, increased with increasing wetland within 200m, these results are surprising. This may suggest that *A. carlini* is not the host of *N. luteoloides* (or not the only host), but development of models more relevant to cleptoparasitic species (such as occupancy and abundance of potential hosts) would be necessary to make a sound prediction.

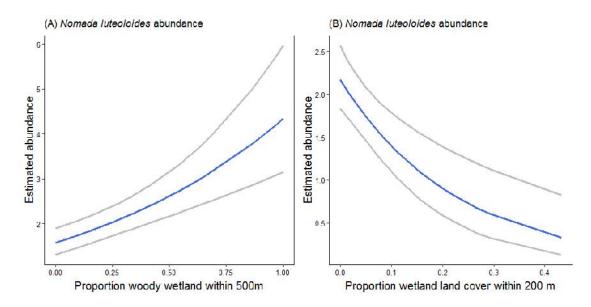


Figure 2.13: Predicted abundance of *N. luteoloides* and SE based on the best fit abundance models. Only the global model met our selection criterion of detlaAIC<2, but the two next best fitting models, woody wetland cover within 500m (A) and wetland land cover within 200m (B) were both significant at p<0.05.

2.3.5 Osmia taurus Occupancy and Abundance

Our most widespread species (found in over 90% of sites), *O. taurus* does not seem particularly sensitive to shifts in landscape composition. Occupancy model comparison yielded several models fitting the selection criterion, but the third best fit model was the null model containing only week and temperature (Table 2.9). The two best fit models were wetland land cover within 200m and open land cover within 500m (Table 2.9).

Table 2.9: Model selection results for *O. taurus* occupancy models, ranked by deltaAIC. Models including the covariates wetland cover within 200m and 500m, open land cover within 500m and 1000m, wetland land cover within 200m and 500m, forest land cover within 1000m and the null model met the selection criterion of deltaAIC<2. Detection covariates temperature and week number were included in all models.

model	nPars	AIC	delta	AICwt	cumltvWt
wetland200	5	2001.8312	0.0000	0.1572	0.1572
open500	5	2002.8728	1.0416	0.0934	0.2505
null	4	2003.0167	1.1855	0.0869	0.3374
open1000	5	2003.1724	1.3412	0.0804	0.4178
forest1000	5	2003.4212	1.5900	0.0710	0.4888
wetland500	5	2003.6523	1.8211	0.0632	0.5520
year	5	2003.9159	2.0847	0.0554	0.6074
open200	5	2004.1813	2.3502	0.0485	0.6560
wetland1000	5	2004.5746	2.7435	0.0399	0.6958
forest500	5	2004.5808	2.7497	0.0397	0.7356
woodywetland1000	5	2004.7727	2.9416	0.0361	0.7717
developed200	5	2004.7962	2.9650	0.0357	0.8074
developed1000	5	2004.9894	3.1583	0.0324	0.8398
woodywetland500	5	2005.0034	3.1723	0.0322	0.8720
woodywetland200	5	2005.0050	3.1738	0.0322	0.9041
forest200	5	2005.0090	3.1778	0.0321	0.9362
developed500	5	2005.0164	3.1853	0.0320	0.9682
elevation	5	2005.0245	3.1934	0.0318	1.0000
global	21	2024.0003	22.1692	0.0000	1.0000

Wetland cover within 200m was positive but not significant (Fig. 2.14A; p=0.19). Open landcover was negatively associated with *O. taurus* occupancy, although this relationship was also not significant (Fig. 2.14B; p=0.14). This exotic

species has spread rapidly throughout the region since its introduction, and appears to have established itself in most wooded habitats of the Mid-Atlantic. The ability of *O*. *taurus* to inhabit woodlots ranging from small urban forest patches to larger state forests does not bode well for its native relatives if indeed there is competition for forage or nesting resources between species.

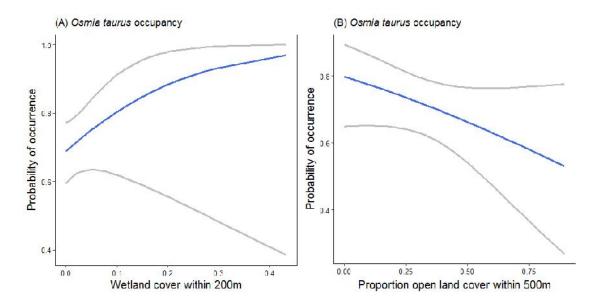


Figure 2.14: Predicted probability of *O. taurus* occurrence and SE based on the best fit occupancy models. The models including wetland within a 200m buffer (A; p=0.19) and open land cover within 500m (B; p=0.14) met our selection criterion of deltaAIC<2, but neither was significant at p<0.05.

Abundance modeling for *O. taurus* yielded similar results, with no one variable strongly predicting the number of bees collected in a woodlot. The best fit model and the only model to meet the selection criterion was the global model containing all covariates (Table 2.10).

Table 2.10:Model selection results for *O. taurus* abundance models, ranked by
deltaAIC. Only the global model met the selection criterion of
deltaAIC<2. Detection covariates temperature and week number were
included in all models.

model	nPars	AIC	delta	AICwt	cumltvWt
global	21	6084.2288	0.0000	0.6426	0.6426
wetland1000	5	6087.1757	2.9468	0.1472	0.7899
woodywetland1000	5	6089.1550	4.9261	0.0547	0.8446
forest1000	5	6090.3738	6.1450	0.0298	0.8743
null	4	6091.6425	7.4136	0.0158	0.8901
developed1000	5	6091.9225	7.6936	0.0137	0.9038
woodywetland500	5	6092.4132	8.1844	0.0107	0.9146
forest500	5	6092.4247	8.1958	0.0107	0.9252
open1000	5	6092.7909	8.5621	0.0089	0.9341
woodywetland200	5	6093.0257	8.7969	0.0079	0.9420
developed200	5	6093.2633	9.0345	0.0070	0.9491
wetland200	5	6093.2952	9.0664	0.0069	0.9560
wetland500	5	6093.3480	9.1191	0.0067	0.9627
forest200	5	6093.3584	9.1295	0.0067	0.9694
developed500	5	6093.4043	9.1755	0.0065	0.9759
open200	5	6093.4645	9.2357	0.0063	0.9823
year	5	6093.5715	9.3426	0.0060	0.9883
elevation	5	6093.6180	9.3892	0.0059	0.9941
open500	5	6093.6264	9.3976	0.0059	1.0000

Of the next best fit models after the global model, both wetland cover within 1000m and woody wetland cover within 1000m significantly predicted *O. taurus* abundance (Fig. 2.15). Abundance increased with increasing wetland cover within 1000m (Fig. 2.15A; p=0.01) but decreased with increasing woody wetland cover (Fig. 2.15B; p=0.04). As discussed with *A. carlini*, we expect that wetland cover opens up the forest canopy and increases area of forest edge, which seems to be preferred by many bee species. However, decreasing abundance with increasing woody wetlands does not seem to fit our earlier prediction that stem nesting species do well in frequently flooded, open woodlots. However, it may be that the lower density of stems

in open woodlots limits nesting resources for these species. In the lower Delmarva sites (with high woody wetland cover), where we saw few bees overall, *Osmia* spp. were present but it low numbers. While these types of sites do not necessarily seem to restrict occupancy of *O. taurus*, they do limit abundance.

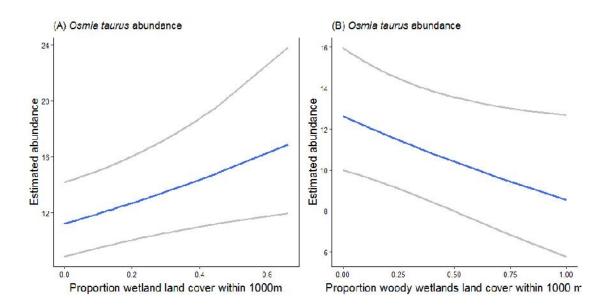


Figure 2.15: Predicted *O. taurus* abundance and SE based on the best fit abundance models. Only the global model met our selection criterion of deltaAIC<2, but wetland cover within 1000m (p=0.01) and woody wetland cover within 1000m (p=0.04) were both significant at p<0.05.

2.3.6 Osmia pumila Occupancy and Abundance

Like *O. taurus*, *O. pumila* occupancy results were fairly uninformative. All models except open landcover within 1000m and the global model met the selection criterion, and the best fit model was the null model containing only week and temperature (Table 2.11). None of the models significantly predicted *O. pumila*

occupancy. Like *O.taurus*, *O. pumila* was common and widespread, and occupancy may depend more on small scale site characteristics than land cover composition.

model	nPars	AIC	delta	AICwt	cumltvWt
null	4	1140.0422	0.0000	0.1123	0.1123
developed200	5	1140.4544	0.4122	0.0914	0.2038
developed500	5	1140.7665	0.7243	0.0782	0.2820
developed1000	5	1141.2731	1.2309	0.0607	0.3427
wetland1000	5	1141.3751	1.3329	0.0577	0.4004
wetland500	5	1141.5924	1.5502	0.0518	0.4521
woodywetland500	5	1141.6722	1.6300	0.0497	0.5019
open200	5	1141.6786	1.6364	0.0496	0.5514
open500	5	1141.7216	1.6794	0.0485	0.5999
year	5	1141.7494	1.7072	0.0478	0.6478
forest200	5	1141.7549	1.7127	0.0477	0.6955
woodywetland200	5	1141.7677	1.7255	0.0474	0.7429
forest500	5	1141.9025	1.8603	0.0443	0.7872
woodywetland1000	5	1141.9290	1.8868	0.0437	0.8310
forest1000	5	1141.9458	1.9036	0.0434	0.8743
elevation	5	1141.9933	1.9511	0.0424	0.9167
wetland200	5	1142.0113	1.9691	0.0420	0.9587
open1000	5	1142.0422	2.0000	0.0413	1.0000
global	21	1168.5278	28.4856	0.0000	1.0000

Table 2.11:Model selection results for *O. pumila* occupancy models, ranked by
deltaAIC. All models except open land cover within 1000m and the
global model met the selection criterion of deltaAIC<2. Detection
covariates temperature and week number were included in all models.

As in *O. taurus*, wetland cover within 1000m was the best fit model of *O. pumila* abundance (Table 2.12). No other models met the selection criterion.

Table 2.12:Model selection results for *O. pumila* abundance models, ranked by
deltaAIC. The model of wetland cover within 1000m met the selection
criterion of deltaAIC<2. Detection covariates temperature and week
number were included in all models.

model	nPars	AIC	delta	AICwt	cumltvWt
wetland1000	5	1415.8468	0.0000	0.3031	0.3031
wetland500	5	1418.1293	2.2825	0.0968	0.4000
developed500	5	1418.9113	3.0645	0.0655	0.4655
developed1000	5	1419.0914	3.2446	0.0599	0.5253
null	4	1419.1617	3.3149	0.0578	0.5831
developed200	5	1419.3424	3.4956	0.0528	0.6359
open500	5	1419.3855	3.5388	0.0517	0.6876
forest1000	5	1419.6111	3.7644	0.0462	0.7337
open200	5	1420.0756	4.2289	0.0366	0.7703
forest500	5	1420.3954	4.5486	0.0312	0.8015
wetland200	5	1420.4639	4.6171	0.0301	0.8316
elevation	5	1420.4788	4.6321	0.0299	0.8615
open1000	5	1420.7321	4.8853	0.0264	0.8879
year	5	1420.8843	5.0376	0.0244	0.9123
forest200	5	1421.0354	5.1886	0.0226	0.9350
woodywetland500	5	1421.0614	5.2147	0.0224	0.9573
woodywetland200	5	1421.1488	5.3020	0.0214	0.9787
woodywetland1000	5	1421.1593	5.3125	0.0213	1.0000
global	21	1435.5487	19.7019	0.0000	1.0000

Wetland cover within 1000m was positively associated with *O. pumila* abundance (Fig. 2.16; p=0.02). Tied with this species' preference for forest edges, these results support our suggestion that wetlands increase edge area, creating ideal habitat for species preferring open canopy forest. Native and non-native *Osmia* had similar responses to land cover variables, which is not surprising given their similar ecology and likely similar foraging and nesting requirements. If these resources are limited, competition between native and exotic *Osmia* seems likely.

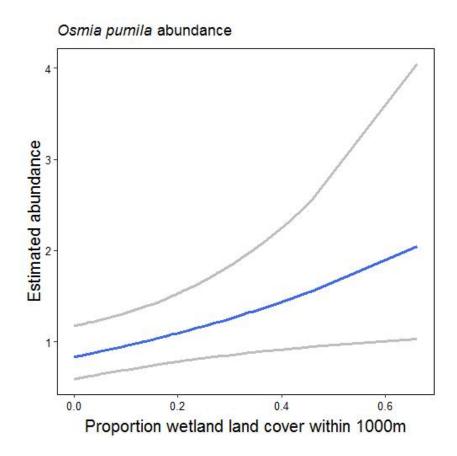


Figure 2.16: Predicted *O. pumila* abundance and SE based on the best fit occupancy model. Wetland cover within 1000m was significant at p<0.05.

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Appendix A

ADDITIONAL SITE INFORMATION

A.1 Site Locations, land covers and diversity measures. Listed by site ID number. Site location in decimal degrees; Percent forest cover within 1000m; Percent woody wetlands within 1000m; Percent open land cover within 1000m; percent developed within 1000m; percent wetland within 1000m; Elevation (m); Abundance for both sampling years; Richness (number of species detected) for both sampling years; Shannon Diversity Index (H) for both sampling years. (See methods for explanation of land cover variables and calculation of H; "-" indicates a site was not sampled in that year.)

Site ID	lat, long	Elv	For.	Woody	Open	Devl.	Wetl.	Ab	un.	Ri	ch.	H	H
		(m)		wet.				2014	2015	2014	2015	2014	2015
Site 1	39.3115,-76.1768	12	25%	17%	31%	0%	28%	134	111	26	26	2.54	2.86
Site 2	39.4481,-77.7285	119	36%	1%	58%	1%	4%	184	-	23	-	2.21	-
Site 3	39.4759,-77.7502	144	2%	0%	95%	3%	0%	134	-	27	-	2.32	-
Site 4	39.0758,-76.6075	16	40%	5%	18%	4%	33%	8	10	7	8	1.91	2.03
Site 5	39.4213,-77.2059	159	25%	7%	67%	1%	0%	419	325	34	21	2.38	1.71
Site 6	38.4917,-76.5914	23	56%	21%	20%	1%	2%	86	90	18	19	2.42	2.18
Site 7	38.4916,-76.592	23	56%	21%	20%	1%	2%	13	-	6	-	1.59	-
Site 8	39.0035,-77.0869	86	17%	1%	40%	42%	0%	24	-	12	-	2.33	-
Site 9	39.2441,-75.7184	23	8%	47%	45%	0%	0%	34	37	19	22	2.82	2.81

Sit	te 10	39.2677,-76.8119	106	37%	0%	35%	28%	0%	52	-	17	-	2.36	-
Sit	te 11	38.97,-76.5681	19	35%	4%	21%	26%	14%	6	-	4	-	1.33	-
Sit	te 12	39.4476,-76.9277	170	39%	0%	58%	3%	0%	80	-	26	-	2.89	-
Sit	te 13	39.3921,-77.5663	126	32%	2%	64%	0%	2%	252	291	25	31	1.81	1.87
Sit	te 14	39.5609,-75.9147	54	68%	2%	30%	0%	0%	35	101	14	28	1.75	2.44
Sit	te 15	39.6736,-75.9314	99	37%	4%	59%	1%	0%	33	28	15	13	2.49	2.41
Sit	te 16	39.6783,-76.9067	258	32%	1%	67%	1%	0%	71	150	24	28	2.30	2.66
Sit	te 17	38.5488,-77.2164	19	52%	10%	11%	1%	26%	-	187	-	32	-	2.59
Sit	te 18	38.5502,-77.2321	5	8%	17%	6%	3%	66%	-	37	-	15	-	2.24
Sit	te 19	39.2347,-76.0079	3	8%	3%	44%	0%	45%	44	48	23	22	2.98	2.87
Sit	te 20	39.2351,-75.985	5	17%	6%	49%	1%	27%	20	-	13	-	2.36	-
Sit	te 21	39.2215,-75.9777	15	24%	5%	68%	1%	2%	39	-	20	-	2.73	-
Sit	te 22	38.4958,-75.3115	17	0%	100%	0%	0%	0%	8	-	8	-	2.08	-
Sit	te 23	38.4926,-75.3168	18	0%	91%	9%	0%	0%	5	6	2	5	0.50	1.56
Sit	te 24	39.0331,-76.42	13	31%	39%	22%	3%	5%	16	73	11	23	2.18	2.93
Sit	te 25	39.0322,-76.4153	13	30%	40%	13%	4%	13%	57	128	20	20	2.53	2.28
Sit	te 26	39.4711,-77.0453	238	29%	3%	68%	1%	0%	183	-	36	-	2.75	-
Sit	te 27	38.5579,-75.8738	11	23%	16%	59%	0%	2%	18	21	10	10	2.11	1.96
Sit	te 28	38.3381,-76.5974	33	56%	16%	26%	2%	0%	70	27	20	13	2.33	2.40
Sit	te 29	39.5763,-75.9138	62	81%	1%	18%	0%	0%	83	114	16	19	1.85	1.58
Sit	te 30	39.6145,-79.1149	753	86%	0%	13%	0%	0%	456	134	30	22	2.26	2.47
Sit	te 31	39.5556,-75.8434	15	31%	7%	42%	3%	18%	17	15	12	5	2.34	1.34
Sit	te 32	39.7009,-78.9461	839	82%	1%	15%	0%	0%	131	150	30	30	2.69	2.46
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Appendix	A.1	continued
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Site 33	38.4459,-76.4584	26	48%	20%	4%	0%	24%	89	46	20	18	2.37	2.26
									-				2.20
Site 34	38.9607,-77.0153	74	1%	0%	9%	89%	0%	64	-	14	-	1.43	-
Site 35	38.9519,-77.0042	69	6%	0%	18%	76%	0%	128	-	25	-	2.10	-
Site 36	38.4974,-75.2618	21	0%	83%	15%	0%	1%	2	-	2	-	0.69	-
Site 37	39.4026,-77.2784	131	40%	3%	57%	1%	0%	11	231	1	29	0.00	2.27
Site 38	38.9913,-76.4553	4	12%	10%	31%	7%	41%	28	32	15	16	2.51	2.30
Site 39	38.4472,-75.1158	3	4%	12%	31%	13%	40%	2	-	2	-	0.69	-
Site 40	39.4911,-76.3422	73	48%	5%	31%	14%	2%	276	-	32	-	2.67	-
Site 41	39.4827,-76.3412	63	44%	5%	32%	14%	5%	107	-	22	-	2.65	-
Site 42	39.5603,-76.2923	110	37%	2%	49%	12%	0%	53	-	25	-	2.89	-
Site 43	38.373,-76.467	20	56%	8%	25%	1%	10%	21	26	10	17	1.92	2.61
Site 44	38.5499,-77.204	29	67%	3%	8%	1%	20%	43	-	17	-	2.16	-
Site 45	38.5461,-77.2025	39	80%	3%	12%	1%	5%	34	-	17	-	2.45	-
Site 46	38.5528,-77.196	23	57%	9%	6%	1%	28%	76	-	20	-	2.55	-
Site 47	38.6239,-76.6684	18	48%	9%	12%	0%	31%	57	65	22	21	2.70	2.34
Site 48	38.2657,-76.6116	30	48%	5%	38%	9%	0%	16	-	7	-	1.66	-
Site 49	38.2688,-76.6144	31	43%	3%	44%	10%	0%	10	-	6	-	1.70	-
Site 50	39.1339,-75.4421	8	2%	34%	62%	1%	1%	4	2	4	2	1.39	0.69
Site 51	38.8638,-75.8388	9	29%	18%	22%	1%	29%	19	-	12	-	2.31	-
Site 52	38.8601,-75.8393	9	30%	18%	17%	0%	34%	17	-	10	-	2.15	-
Site 53	38.7225,-76.7113	16	35%	6%	58%	0%	1%	50	-	18	-	2.45	-
Site 54	38.728,-76.7156	27	55%	1%	43%	0%	0%	46	-	17	-	2.20	-
Site 55	39.4134,-77.1993	168	43%	3%	53%	0%	0%	1	-	1	-	0.00	-
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Appendix A.1 continued

Site 56	38.448,-75.1364	10	15%	35%	33%	8%	10%	4	18	3	7	1.04	1.53
Site 57	38.2351,-75.4551	16	35%	40%	25%	0%	0%	16	-	8	-	1.84	-
Site 58	38.243,-75.469	16	34%	50%	14%	0%	1%	6	-	4	-	1.24	-
Site 59	39.645,-76.0876	124	43%	2%	54%	1%	0%	80	-	24	-	2.49	-
Site 60	38.913,-77.0981	39	21%	6%	27%	28%	18%	24	99	11	19	2.16	2.27
Site 61	39.2842,-77.5507	101	59%	2%	16%	0%	22%	18	-	9	-	1.96	-
Site 62	39.2851,-77.5488	116	61%	2%	17%	0%	19%	21	-	7	-	1.44	-
Site 63	39.3233,-77.6637	92	29%	9%	27%	10%	25%	8	-	3	-	0.74	-
Site 64	39.3249,-77.6644	97	29%	9%	27%	11%	24%	41	-	12	-	1.78	-
Site 65	38.9782,-77.1713	68	37%	4%	42%	15%	1%	241	-	23	-	2.21	-
Site 66	38.9716,-77.1729	38	41%	7%	27%	11%	13%	458	-	24	-	2.18	-
Site 67	39.0979,-77.4697	69	34%	13%	29%	2%	22%	155	-	21	-	2.12	-
Site 68	39.1053,-77.4711	77	33%	11%	37%	0%	19%	122	-	24	-	2.53	-
Site 69	39.1035,-77.4716	74	33%	13%	33%	0%	21%	128	-	22	-	2.31	-
Site 70	39.3456,-77.7482	135	63%	0%	17%	1%	19%	356	200	24	19	1.65	1.24
Site 71	39.3488,-77.744	134	62%	0%	18%	2%	18%	138	-	17	-	1.54	-
Site 72	39.3781,-77.7486	111	64%	0%	15%	1%	21%	214	-	26	-	2.52	-
Site 73	39.3811,-77.7501	113	66%	0%	16%	1%	18%	125	-	14	-	2.22	-
Site 74	39.4511,-76.2673	18	28%	4%	18%	15%	34%	29	23	13	12	2.01	2.30
Site 75	38.9778,-75.5871	36	8%	20%	71%	1%	0%	10	-	3	-	0.80	-
Site 76	38.9728,-76.9594	15	13%	5%	18%	64%	0%	-	63	-	18	-	2.52
Site 77	38.8544,-76.12	7	14%	36%	48%	0%	2%	18	50	3	13	0.43	1.63
Site 78	38.5271,-75.7256	8	27%	16%	54%	3%	0%	12	34	8	10	1.98	1.63

Appendix A.1 contin	ued
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Site 79	38.2602,-76.4306	27	54%	12%	23%	8%	2%	63	-	20	-	2.58	-
Site 80	38.2703,-76.4354	20	39%	6%	27%	25%	3%	33	-	17	-	2.62	-
Site 81	36.704,-75.992	4	0%	34%	60%	1%	5%	3	-	3	-	1.10	-
Site 82	36.703,-75.991	5	0%	35%	61%	1%	3%	2	-	2	-	0.69	-
Site 83	39.1909,-76.8948	105	44%	0%	33%	23%	0%	68	131	19	27	2.53	2.34
Site 84	38.9858,-77.0458	81	44%	2%	23%	30%	0%	246	217	34	29	2.54	2.20
Site 85	38.9595,-77.0504	86	63%	0%	26%	11%	0%	187	225	32	35	2.43	2.58
Site 86	38.9807,-77.0424	89	57%	2%	21%	21%	0%	142	186	28	27	2.78	2.45
Site 87	38.4762,-75.3173	16	0%	62%	37%	1%	0%	-	12	-	6	-	1.66
Site 88	39.2128,-76.9176	125	56%	6%	31%	7%	0%	79	-	24	-	2.66	-
Site 89	38.3986,-75.2263	11	9%	21%	66%	3%	0%	30	-	10	-	1.36	-
Site 90	39.3524,-75.9904	19	27%	6%	51%	0%	15%	191	-	35	-	2.91	-
Site 91	39.5242,-76.1226	18	28%	17%	41%	14%	0%	79	-	20	-	1.85	-
Site 92	39.5214,-76.1071	13	7%	5%	49%	1%	37%	165	-	19	-	1.41	-
Site 93	38.8665,-75.7229	19	10%	32%	57%	0%	1%	10	-	10	-	2.30	-
Site 94	38.9838,-77.0029	75	20%	0%	35%	45%	0%	118	-	29	-	2.59	-
Site 95	38.9715,-75.9489	12	1%	22%	72%	0%	5%	36	-	18	-	2.61	-
Site 96	38.9457,-75.9396	15	23%	27%	50%	0%	0%	42	-	15	-	2.26	-
Site 97	39.6473,-79.0173	747	92%	0%	7%	0%	0%	253	-	46	-	3.05	-
Site 98	38.7193,-76.6455	28	52%	16%	30%	2%	0%	-	76	-	26	-	2.70
Site 99	38.1327,-76.4334	7	20%	16%	14%	4%	46%	39	-	19	-	2.58	-
Site 100	38.3419,-75.8269	8	15%	70%	15%	0%	0%	15	15	9	5	2.06	1.40
Site 101	39.0442,-75.6336	21	11%	52%	36%	0%	0%	31	-	12	-	2.21	-
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Site 102	38.9393,-77.2628	102	40%	2%	31%	27%	0%	83	-	24	-	2.59	-
Site 103	38.9402,-77.2627	103	40%	2%	32%	27%	0%	54	-	19	-	2.53	-
Site 104	39.3215,-76.8124	115	71%	2%	24%	2%	1%	87	105	28	26	3.03	2.83
Site 105	38.9391,-76.0816	13	7%	9%	79%	2%	3%	44	-	14	-	2.34	-
Site 106	39.6953,-75.9078	119	25%	0%	73%	2%	0%	57	-	17	-	1.93	-

Appendix B

ADDITIONAL INFORMATION ON BEE SPECIES

B.1 Life history information for all species collected. Families are organized taxonomically, species are alphabetical within family. Number of total individuals captured across both years (n); Nesting substrate (S=soil, W=wood, C=cavity, P=stem pitch, H=hive); Pollen specificity (P=polylectic, O=oligolectic); Preferred floral host; Social type (S=solitary or subsocial, P=parasitic, E=eusocial); Native (N) or Exotic (E). In cases where life history information is unknown, it has been inferred from closely related species.

Family	Species	n	Nest	Lecty	Floral Host	Sociality	N/E
Andrenidae							
	Andrena arabis	9	S	0	Brassicaceae	S	Ν
	Andrena atlantica	3	S	Р		S	Ν
	Andrena banksi	16	S	Р		S	Ν
	Andrena barbara	195	S	Р		S	Ν
	Andrena bradleyi	3	S	0	Gaylussacia, Vaccinium	S	Ν
	Andrena brevipalpis	13	S	Р		S	Ν
	Andrena carlini	2641	S	Р		S	Ν
	Andrena carolina	3	S	0	Vaccinium	S	Ν
	Andrena commoda	2	S	Р		S	Ν
	Andrena confederata	3	S	Р		S	Ν
	Andrena cornelli	11	S	0	Rhododendron	S	Ν
	Andrena cressonii	87	S	Р		S	Ν
	Andrena dunningi	5	S	Р		S	Ν

Andrena erigeniae	782	S	0	Claytonia	S	Ν
Andrena erythronii	6	S	0	Erythronium	S	Ν
Andrena fenningeri	2	S	Р		S	Ν
Andrena forbesii	12	S	Р		S	Ν
Andrena heraclei	10	S	Р		S	Ν
Andrena hilaris	4	S	Р		S	Ν
Andrena ilicis	2	S	Р		S	Ν
Andrena illini	77	S	Р		S	Ν
Andrena imitatrix	3	S	Р		S	Ν
Andrena macra	1	S	Р		S	Ν
Andrena mandibularis	38	S	Р		S	Ν
Andrena miserabilis	25	S	Р		S	Ν
Andrena morrisonella	10	S	Р		S	Ν
Andrena nasonii	435	S	Р		S	Ν
Andrena nida	1	S	Р		S	Ν
Andrena nivalis	1	S	Р		S	Ν
Andrena nuda	3	S	Р		S	Ν
Andrena perplexa	1079	S	Р		S	Ν
Andrena personata	28	S	Р		S	Ν
Andrena pruni	303	S	Р		S	Ν
Andrena rufosignata	23	S	Р		S	Ν
Andrena rugosa	24	S	Р		S	Ν

	Andrena sayi	2	S	Р		S	Ν
	Andrena tridens	126	S	Р		S	Ν
	Andrena vicina	57	S	Р		S	Ν
	Andrena violae	69	S	0	Viola	S	Ν
	Andrena wilkella	1	S	Р		S	E
	Andrena ziziaeformis	1	S	Р		S	Ν
	Calliopsis andreniformis	2	S	Р		S	Ν
Colletidae							
	Colletes inaequalis	25	S	Р		S	Ν
	Colletes thoracicus	2	S	Р		S	Ν
	Colletes validus	1	S	Р	prefers Vaccinium	S	Ν
	Hylaeus affinis/modestus	1	С	Р		S	Ν
	Hylaeus annulatus	1	С	Р		S	Ν
Halictidae							
	Agapostemon texanus	4	S	Р		S	Ν
	Agapostemon virescens	9	S	Р		S	Ν
	Augochlora pura	162	W	Р		S	Ν
	Augochlorella aurata	29	S	Р		Е	Ν
	Augochloropsis metallica	4	S	Р		S	Ν
	Halictus confusus	19	S	Р		Е	Ν
	Halictus parallelus	5	S	Р		S	Ν
	Halictus poeyi/ligatus	4	S	Р		S	Ν

Appendix B.1

Halictus rubicundus	35	S	Р	Е	Ν
Lasioglossum abanci	70	S	Р	Е	Ν
Lasioglossum acuminatum	2	S	Р	S	Ν
Lasioglossum admirandum	5	S	Р	Е	Ν
Lasioglossum birkmanni	12	S	Р	S	Ν
Lasioglossum bruneri	5	S	Р	Е	Ν
Lasioglossum callidum	1	S	Р	S	Ν
Lasioglossum cattellae	14	S	Р	Е	Ν
Lasioglossum coeruleum	75	W	Р	Е	Ν
Lasioglossum comagenense	1	S	Р	S	Ν
Lasioglossum coreopsis	1	S	Р	Е	Ν
Lasioglossum coriaceum	30	S	Р	S	Ν
Lasioglossum cressonii	93	W	Р	Е	Ν
Lasioglossum ephialtum	4	S	Р	Е	Ν
Lasioglossum floridanum	2	S	Р	S	Ν
Lasioglossum foxii	6	S	Р	S	Ν
Lasioglossum fuscipenne	20	S	Р	S	Ν
Lasioglossum gotham	212	S	Р	S	Ν
Lasioglossum heterognathum	1	S	Р	Е	Ν
Lasioglossum hitchensi	22	S	Р	S	Ν
Lasioglossum illinoense	3	S	Р	Е	Ν
Lasioglossum imitatum	38	S	Р	Е	Ν

Appendix B.1

	Lasioglossum leucozonium	1	S	Р	S	Е
	Lasioglossum lineatulum	1	S	Р	E	Ν
	Lasioglossum macoupinense	2	S	Р	S	Ν
	Lasioglossum nelumbonis	1	S	Р	S	Ν
	Lasioglossum nigroviride	2	S	Р	E	Ν
	Lasioglossum nymphaearum	1	S	Р	E	Ν
	Lasioglossum oblongum	12	W	Р	E	Ν
	Lasioglossum obscurum	1	S	Р	S	Ν
	Lasioglossum pectorale	4	S	Р	S	Ν
	Lasioglossum platyparium	4	S	Р	Р	Ν
	Lasioglossum quebecense	395	S	Р	S	Ν
	Lasioglossum smilacinae	7	S	Р	S	Ν
	Lasioglossum subviridatum	107	S	Р	E	Е
	Lasioglossum tegulare	8	S	Р	E	Ν
	Lasioglossum trigeminum	1	S	0	S	Ν
	Lasioglossum versans	42	S	Р	E	Ν
	Lasioglossum versatum	4	S	Р	E	Ν
	Lasioglossum weemsi	11	S	Р	S	Ν
	Lasioglossum zephyrum	5	S	Р	S	Ν
	Sphecodes species	15	S	Р	Р	Ν
Megachilidae						
	Hoplitis producta	1	С	Р	S	Ν

Appendix B.1

	Osmia atriventris	90	С	Р		S	Ν
	Osmia bucephala	20	С	Р		S	Ν
	Osmia collinsiae	19	С	Р		S	Ν
	Osmia cornifrons	361	С	Р		S	Е
	Osmia georgica	41	С	Р		S	Ν
	Osmia inspergens	2	С	Р		S	Ν
	Osmia lignaria	10	С	Р		S	Ν
	Osmia pumila	186	С	Р		S	Ν
	Osmia taurus	1014	С	Р		S	Е
	Osmia virga	9	С	0	Vaccinium	S	Ν
Apidae	~						
	Anthophora plumipes	13	S	Р		S	Е
	Apis mellifera	106	Н	Р		E	Е
	Bombus bimaculatus	21	Н	Р		Е	Ν
	Bombus citrinus	2	Н	Р		Р	Ν
	Bombus fervidus	3	Н	Р		Е	Ν
	Bombus griseocollis	17	Н	Р		Е	Ν
	Bombus impatiens	48	Н	Р		Е	Ν
	Bombus pensylvanicus	1	Н	Р		Е	Ν
	Bombus perplexus	5	Н	Р		Е	Ν
	Bombus sandersoni	6	Н	Р		Е	Ν
	Bombus vagans	1	Н	Р		Е	Ν

Ceratina calcarata	503	Р	Р		S	Ν
Ceratina dupla	38	Р	Р		S	Ν
Ceratina mikmaqi	6	Р	Р		S	Ν
Ceratina strenua	28	Р	Р		S	Ν
Eucera atriventris	2	S	Р		S	Ν
Eucera hamata	1	S	Р		S	Ν
Eucera rosae	2	S	Р		S	Ν
Habropoda laboriosa	59	S	Ο	Vaccinium, Cercis	S	Ν
Nomada annulata	3	S	Р		Р	Ν
Nomada armatella	2	S	Р		Р	Ν
Nomada articulata	1	S	Р		Р	Ν
Nomada australis	1	S	Р		Р	Ν
Nomada bidentate/group	259	S	Р		Р	Ν
Nomada composita	77	S	Р		Р	Ν
Nomada cressonii	13	S	Р		Р	Ν
Nomada denticulata	35	S	Р		Р	Ν
Nomada depressa	34	S	Р		Р	Ν
Nomada fragariae	2	S	Р		Р	Ν
Nomada gracilis	9	S	Р		Р	Ν
Nomada imbricata	342	S	Р		Р	Ν
Nomada lehighensis	19	S	Р		Р	Ν
Nomada luteola	20	S	Р		Р	Ν

Nomada luteoloides	535	S	Р		Р	Ν
Nomada maculata	116	S	Р		Р	Ν
Nomada perplexa	2	S	Р		Р	Ν
Nomada pygmaea	363	S	Р		Р	Ν
Nomada sayi/illinoensis	30	S	Р		Р	Ν
Nomada sulphurata	43	S	Р		Р	Ν
Xylocopa virginica	4	W	Р		S	Ν

					۲	Week Nı	ımber						
	1	2	3	4	5	6	7	8	9	10	11	12	
Species	March		April				May					June	Tota
Andrendidae													
Andrena arabis	0	0	0	0	0	1	1	2	0	0	0	0	4
Andrena atlantica	0	0	0	0	0	0	0	2	0	0	0	0	2
Andrena banksi	0	0	0	0	1	5	1	1	0	0	0	0	8
Andrena barbara	0	2	3	27	13	37	16	12	3	0	0	0	113
Andrena bradleyi	0	0	0	2	0	0	1	0	0	0	0	0	3
Andrena brevipalpis	0	0	0	1	0	1	5	4	0	0	0	0	11
Andrena carlini	46	107	460	573	259	188	77	39	7	3	1	1	1761
Andrena carolina	0	0	0	0	0	3	0	0	0	0	0	0	3
Andrena commoda	0	0	0	0	0	0	0	1	0	1	0	0	2
Andrena confederata	0	0	0	0	0	2	0	0	0	0	0	0	2
Andrena cornelli	0	0	0	0	0	3	3	2	0	0	0	0	8
Andrena cressonii	3	1	3	3	2	29	9	8	2	2	1	0	63
Andrena dunningi	0	0	0	2	1	1	0	1	0	0	0	0	5
Andrena erigeniae	37	26	33	79	126	71	33	26	47	21	2	0	501
Andrena erythronii	0	0	0	1	0	0	2	0	0	1	2	0	6
Andrena fenningeri	0	0	0	1	0	0	0	0	0	0	0	0	1

B.2 Abundance by week for all species collected in 2014. Families are organized taxonomically, species are alphabetical within family.

													ı I
Andrena forbesii	0	0	0	1	2	3	0	5	0	0	1	0	12
Andrena heraclei	0	0	0	0	1	2	1	0	0	0	1	0	5
Andrena hilaris	0	0	0	0	1	3	0	0	0	0	0	0	4
Andrena illini	0	0	3	4	4	22	2	2	2	0	0	0	39
Andrena imitatrix	0	0	0	0	0	1	0	0	0	0	0	0	1
Andrena macra	0	0	0	0	0	0	0	1	0	0	0	0	1
Andrena mandibularis	0	0	2	11	5	8	2	0	0	0	0	0	28
Andrena miserabilis	0	1	0	7	3	3	2	2	1	0	0	0	19
Andrena morrisonella	0	0	0	0	0	2	0	0	0	0	0	0	2
Andrena nasonii	0	3	4	24	31	123	52	69	19	6	1	0	332
Andrena nida	0	0	0	0	0	0	0	1	0	0	0	0	1
Andrena nuda	0	0	0	0	1	0	1	0	0	0	0	0	2
Andrena perplexa	0	0	11	31	33	260	225	201	38	8	2	1	810
Andrena personata	0	0	0	1	0	0	5	6	2	2	0	0	16
Andrena pruni	1	1	1	1	65	120	19	48	4	3	0	0	263
Andrena rufosignata	0	0	0	1	0	7	4	0	0	0	1	0	13
Andrena rugosa	0	2	2	4	3	1	2	2	1	1	1	0	19
Andrena sayi	0	0	0	0	0	0	1	0	0	0	0	0	1
Andrena tridens	1	4	12	44	11	16	7	3	0	0	1	0	99
Andrena vicina	0	0	1	2	3	17	9	6	2	0	1	0	41
Andrena violae	0	1	0	5	5	2	4	2	6	2	0	0	27
Andrena wilkella	0	0	0	0	0	0	0	0	0	0	1	0	1
Andrena ziziaeformis	0	0	0	0	0	0	0	0	1	0	0	0	1

r		1												
Colletidae														
	Colletes inaequalis	1	0	2	3	1	1	2	1	0	0	0	0	11
	Colletes thoracicus	0	0	0	0	0	0	0	0	1	0	0	0	1
	Colletes validus	0	0	0	0	0	1	0	0	0	0	0	0	1
	Hylaeus annulatus	0	0	0	0	0	0	0	0	0	0	0	1	1
Halictidae														
	Agapostemon texanus	0	0	0	0	0	1	1	0	0	0	0	0	2
	Agapostemon virescens	0	0	0	0	0	2	1	0	1	0	0	0	4
	Augochlora pura	0	1	0	12	13	30	10	19	6	2	2	0	95
	Augochlorella aurata	0	0	0	2	1	2	4	2	0	3	0	0	14
	Augochloropsis metallica	0	0	1	2	0	0	1	0	0	0	0	0	4
	Halictus confusus	0	0	0	0	0	4	3	3	3	1	0	0	14
	Halictus parallelus	0	0	0	2	1	0	0	2	0	0	0	0	5
	Halictus poeyi_ligatus	0	0	0	1	2	0	1	0	0	0	0	0	4
	Halictus rubicundus	0	1	2	10	5	5	5	1	0	0	1	0	30
	Hoplitis producta	0	0	0	0	0	0	0	0	0	1	0	0	1
	Lasioglossum abanci	0	0	10	25	9	5	1	1	0	0	0	0	51
	Lasioglossum acuminatum	0	0	0	1	0	0	0	1	0	0	0	0	2
	Lasioglossum admirandum		1	2	1	0	1	0	0	0	0	0	0	5
	Lasioglossum birkmanni	0	0	0	1	1	1	2	2	0	0	0	0	7
	Lasioglossum bruneri		0	1	0	1	0	0	0	0	0	0	0	2
	Lasioglossum cattellae	İ	0	0	3	0	3	2	2	2	0	0	0	12
	Lasioglossum coeruleum		0	9	19	8	5	0	1	1	0	0	0	43
			-	-	-	-	-	-			-	-	-	- 1

Lasioglossum comagenense	0	0	0	0	0	0	1	0	0	0	0	0	1
Lasioglossum coreopsis	0	0	0	0	1	0	0	0	0	0	0	0	1
Lasioglossum coriaceum	0	0	1	0	0	5	6	3	0	3	3	0	21
Lasioglossum cressonii	1	0	4	24	6	10	9	8	4	6	4	0	76
Lasioglossum ephialtum	0	0	0	1	0	0	0	2	1	0	0	0	4
Lasioglossum floridanum	0	0	0	0	1	0	0	0	0	0	0	0	1
Lasioglossum foxii	0	0	0	2	1	2	1	0	0	0	0	0	6
Lasioglossum fuscipenne	0	0	3	5	1	2	4	0	1	0	0	0	16
Lasioglossum gotham	2	23	24	81	9	19	5	2	0	0	1	0	166
Lasioglossum heterognathum	0	0	0	0	0	1	0	0	0	0	0	0	1
Lasioglossum hitchensi	0	4	2	2	0	3	2	3	0	1	0	0	17
Lasioglossum illinoense	0	0	1	0	0	0	0	0	0	0	0	0	1
Lasioglossum imitatum	0	0	1	4	2	5	6	6	3	0	1	0	28
Lasioglossum leucozonium	0	0	0	0	0	0	0	0	1	0	0	0	1
Lasioglossum lineatulum	0	0	0	0	0	0	0	0	0	0	1	0	1
Lasioglossum macoupinense	0	0	0	0	0	2	0	0	0	0	0	0	2
Lasioglossum nigroviride	0	0	0	0	0	1	0	0	0	0	0	0	1
Lasioglossum oblongum	0	0	3	1	1	0	1	1	0	0	0	0	7
Lasioglossum quebecense	0	9	66	169	15	47	16	15	3	2	2	0	344
Lasioglossum smilacinae	2	0	2	1	0	1	0	0	0	1	0	0	7
Lasioglossum subviridatum	0	1	7	25	18	17	4	7	1	0	2	0	82
Lasioglossum tegulare	0	0	0	1	3	1	1	1	0	0	0	0	7
Lasioglossum trigeminum	0	0	0	0	1	0	0	0	0	0	0	0	1

	Lasioglossum versans	0	0	0	3	3	7	7	2	3	4	8	0	37
	Lasioglossum versatum	0	0	0	0	0	1	0	0	0	0	0	0	1
	Lasioglossum weemsi	0	0	0	1	1	0	2	2	1	0	0	0	7
	Lasioglossum zephyrum	0	0	0	1	1	1	0	0	0	0	0	0	3
	Sphecodes species			1	2	0	0	1	0	2	0	0	0	8
Megachildae	î													
	Osmia atriventris	0	1	4	18	5	4	3	0	2	0	2	0	39
	Osmia bucephala	0	0	0	0	1	5	6	0	1	0	1	0	14
	Osmia collinsiae			1	3	3	4	1	2	1	0	0	0	15
	Osmia cornifrons	1	2	24	55	20	65	69	32	2	1	1	0	272
	Osmia georgica		0	0	2	11	9	7	5	0	0	0	0	34
	Osmia inspergens			0	0	1	0	1	0	0	0	0	0	2
	Osmia lignaria			0	2	1	3	0	0	0	0	0	0	6
	Osmia pumila			2	20	29	23	9	10	5	0	0	0	99
	Osmia taurus			17	187	183	111	33	10	7	2	3	0	554
	Osmia virga			0	1	2	1	0	0	, 0	0	0	0	4
Apidae	Osma virga	0	0	0	1	2	1	0	0	0	0	0	0	
Apluae	Authorhoug pluminog	0	0	0	2	2	4	2	0	0	0	0	0	10
	Anthophora plumipes						4	2					-	
	Apis mellifera		1	18	8	5	7	3	4	10	0	1	0	61
	Bombus bimaculatus		0	0	5	3	2	0	0	0	0	0	0	10
	Bombus citrinus		0	0	0	0	2	0	0	0	0	0	0	2
	Bombus fervidus	0	0	0	1	1	0	0	0	0	0	0	0	2
	Bombus griseocollis	0	0	0	4	6	2	2	3	0	0	0	0	17

													1
Bombus impatiens	0	0	1	2	5	1	3	3	0	0	0	0	15
Bombus pensylvanicus	0	0	0	0	1	0	0	0	0	0	0	0	1
Bombus perplexus	0	0	0	0	2	0	0	0	1	1	0	0	4
Bombus sandersoni	0	0	0	0	1	0	2	1	0	0	0	0	4
Bombus vagans	0	0	0	0	0	0	0	1	0	0	0	0	1
Ceratina calcarata	2	1	6	21	48	23	21	82	42	14	4	0	264
Ceratina dupla	0	0	1	0	0	0	0	3	1	0	0	0	5
Ceratina mikmaqi	0	0	0	0	0	0	0	1	0	1	0	0	2
Ceratina strenua	0	0	1	2	2	4	0	1	2	0	0	0	12
Eucera atriventris	0	0	0	0	0	0	1	0	0	0	0	0	1
Eucera hamata	0	0	0	0	0	0	0	1	0	0	0	0	1
Eucera rosae	0	0	0	0	0	0	0	1	1	0	0	0	2
Habropoda laboriosa	0	1	0	20	14	4	4	0	0	0	0	0	43
Nomada annulata	0	0	0	2	0	1	0	0	0	0	0	0	3
Nomada armatella	0	0	0	0	1	1	0	0	0	0	0	0	2
Nomada articulata	0	0	0	0	0	0	0	1	0	0	0	0	1
Nomada australis	0	0	0	0	0	0	0	1	0	0	0	0	1
Nomada bidentate_group	3	16	33	47	16	41	32	20	6	3	0	1	218
Nomada composita	0	5	11	33	3	6	7	8	1	2	0	0	76
Nomada cressonii	0	0	0	2	2	2	0	0	1	1	0	0	8
Nomada denticulata	0	0	0	0	3	11	5	1	1	0	1	0	22
Nomada depressa	0	0	0	0	2	9	9	5	1	0	0	0	26
Nomada gracilis	0	0	0	1	1	0	2	4	0	0	1	0	9

Nomada imbricata	0	0	3	4	1	29	37	95	54	17	1	1	242
Nomada lehighensis	1	0	5	6	0	0	1	0	0	0	0	0	13
Nomada luteola	0	0	1	0	0	4	7	3	0	0	0	1	16
Nomada luteoloides	0	1	4	49	41	127	49	45	7	1	2	1	327
Nomada maculata	0	1	4	1	5	16	12	20	3	3	2	0	67
Nomada perplexa	0	0	0	0	0	0	2	0	0	0	0	0	2
Nomada pygmaea	1	3	7	25	12	93	69	58	4	1	4	0	277
Nomada sayi_illinoensis	0	0	0	1	2	4	3	4	4	4	0	0	22
Nomada sulphurata	0	0	0	1	3	17	4	4	0	0	0	0	29
Xylocopa virginica	0	1	0	0	0	0	0	1	0	1	0	0	3
Total	108	223	820	1755	1114	1752	989	963	326	126	64	7	8247

					Wee	k Nur	nber						
	1	2	3	4	5	6	7	8	9	10	11	12	
Species	March		April				May					June	Total
Andrenidae													
Andrena arabis	0	0	0	4	0	1	0	0	0	0	0	0	5
Andrena atlantica	0	0	0	0	0	0	1	0	0	0	0	0	1
Andrena banksi	0	0	0	0	2	3	2	0	0	1	0	0	8
Andrena barbara	0	2	14	23	17	14	10	0	1	1	0	0	82
Andrena brevipalpis	0	0	0	0	0	1	1	0	0	0	0	0	2
Andrena carlini	20	93	213	242	211	39	35	25	1	0	0	1	880
Andrena confederata	0	0	0	0	0	0	1	0	0	0	0	0	1
Andrena cornelli	0	0	0	0	1	1	1	0	0	0	0	0	3
Andrena cressonii	0	0	1	4	5	8	5	1	0	0	0	0	24
Andrena erigeniae	1	3	14	46	54	20	38	70	32	3	0	0	281
Andrena fenningeri	0	0	1	0	0	0	0	0	0	0	0	0	1
Andrena heraclei	0	0	0	0	0	2	1	1	0	1	0	0	5
Andrena ilicis	0	0	0	0	0	0	2	0	0	0	0	0	2
Andrena illini	0	0	0	21	8	6	3	0	0	0	0	0	38
Andrena imitatrix	0	0	0	0	0	0	0	0	1	0	1	0	2
Andrena mandibularis	0	0	2	3	5	0	0	0	0	0	0	0	10
Andrena miserabilis	0	0	2	0	2	0	2	0	0	0	0	0	6
Andrena morrisonella	0	0	1	1	4	1	1	0	0	0	0	0	8
Andrena nasonii	0	1	2	9	22	42	19	6	2	0	0	0	103
Andrena nivalis	0	0	0	1	0	0	0	0	0	0	0	0	1
Andrena nuda	0	0	0	0	0	0	0	1	0	0	0	0	1

B.3 Abundance by week for all species collected in 2015. Families are organized taxonomically, species are alphabetical within family.

Andrena perplexa	0	0	1	1	40	84	113	12	11	6	1	0	269
Andrena personata	0	0	0	0	1	3	4	2	2	0	0	0	12
Andrena pruni	0	0	0	2	6	7	20	4	0	1	0	0	40
Andrena rufosignata	0	0	5	0	3	0	2	0	0	0	0	0	10
Andrena rugosa	0	0	1	0	2	0	1	0	1	0	0	0	5
Andrena sayi	0	0	0	0	0	1	0	0	0	0	0	0	1
Andrena tridens	0	7	11	3	2	1	3	0	0	0	0	0	27
Andrena vicina	0	0	2	2	2	4	5	1	0	0	0	0	16
Andrena violae	0	0	1	1	5	8	7	18	2	0	0	0	42
Calliopsis andreniformis	0	0	0	0	2	0	0	0	0	0	0	0	2
Colletidae													
Colletes inaequalis	0	0	8	2	1	1	1	1	0	0	0	0	14
Colletes thoracicus	0	0	0	0	0	0	1	0	0	0	0	0	1
Hylaeus affinis_modestus	0	0	0	0	1	0	0	0	0	0	0	0	1
Halictidae													
Agapostemon texanus	0	0	0	0	1	0	1	0	0	0	0	0	2
Agapostemon virescens	0	0	0	0	1	0	1	3	0	0	0	0	5
Augochlora pura	0	0	3	9	24	14	8	6	2	1	0	0	67
Augochlorella aurata	0	0	0	2	2	2	2	3	3	0	1	0	15
Halictus confusus	0	0	0	0	0	1	3	1	0	0	0	0	5
Halictus rubicundus	0	0	1	0	3	0	1	0	0	0	0	0	5
Lasioglossum abanci	0	1	1	5	6	3	1	2	0	0	0	0	19
Lasioglossum birkmanni	0	0	0	2	0	0	1	0	0	1	1	0	5
Lasioglossum bruneri	0	0	0	1	1	0	0	0	1	0	0	0	3
Lasioglossum callidum	0	1	0	0	0	0	0	0	0	0	0	0	1
Lasioglossum cattellae	0	0	0	0	1	1	0	0	0	0	0	0	2
Lasioglossum coeruleum	0	0	9	13	6	2	1	0	0	0	0	1	32

Lasioglossum coriaceum	0	0	0	1	3	0	2	0	2	0	1	0	9
Lasioglossum cressonii	0	1	1	6	2	2	2	1	0	2	0	0	17
Lasioglossum floridanum	0	0	0	0	1	0	0	0	0	0	0	0	1
Lasioglossum fuscipenne	0	0	0	0	1	2	1	0	0	0	0	0	4
Lasioglossum gotham	0	2	21	11	7	2	1	1	0	0	1	0	46
Lasioglossum hitchensi	0	1	1	1	0	1	0	1	0	0	0	0	5
Lasioglossum illinoense	0	0	0	1	0	0	0	0	0	1	0	0	2
Lasioglossum imitatum	0	0	0	3	2	3	1	1	0	0	0	0	10
Lasioglossum nelumbonis	0	0	0	0	0	0	0	0	0	1	0	0	1
Lasioglossum nigroviride	0	0	0	0	0	0	0	1	0	0	0	0	1
Lasioglossum nymphaearum	0	0	0	0	1	0	0	0	0	0	0	0	1
Lasioglossum oblongum	0	0	1	0	1	0	2	0	1	0	0	0	5
Lasioglossum obscurum	0	0	0	0	0	0	0	1	0	0	0	0	1
Lasioglossum pectorale	0	0	0	0	0	0	0	2	1	1	0	0	4
Lasioglossum perplexa	0	0	0	0	0	1	0	0	0	0	0	0	1
Lasioglossum platyparium	0	0	0	2	2	0	0	0	0	0	0	0	4
Lasioglossum quebecense	0	6	3	17	4	8	12	0	0	1	0	0	51
Lasioglossum subviridatum	0	2	6	6	2	2	5	1	0	0	0	1	25
Lasioglossum tegulare	0	0	0	0	1	0	0	0	0	0	0	0	1
Lasioglossum versans	0	0	0	0	0	1	1	3	0	0	0	0	5
Lasioglossum versatum	0	0	0	0	2	1	0	0	0	0	0	0	3
Lasioglossum weemsi	0	1	2	0	0	1	0	0	0	0	0	0	4
Lasioglossum zephyrum	0	0	0	0	0	0	1	0	1	0	0	0	2
Sphecodes species	0	0	2	0	2	0	1	2	0	0	0	0	7
Megachilidae													
Osmia atriventris	0	0	9	14	16	6	3	2	0	1	0	0	51
Osmia bucephala	0	0	0	1	2	2	0	0	1	0	0	0	6

Osmia collinsiae	0	0	0	2	1	0	1	0	0	0	0	0	4
Osmia cornifrons	0	1	2	18	12	23	18	14	0	1	0	0	89
Osmia georgica	0	0	0	1	4	1	1	0	0	0	0	0	7
Osmia lignaria	0	0	0	0	2	1	1	0	0	0	0	0	4
Osmia pumila	0	0	10	31	21	12	6	5	1	1	0	0	87
Osmia taurus	1	2	43	149	190	47	15	10	1	1	0	1	460
Osmia virga	0	0	0	0	3	2	0	0	0	0	0	0	5
Apidae													
Anthophora plumipes	0	0	0	3	0	0	0	0	0	0	0	0	3
Apis mellifera	3	6	8	5	2	17	1	0	0	2	1	0	45
Bombus bimaculatus	0	0	2	2	6	1	0	0	0	0	0	0	11
Bombus fervidus	0	0	0	0	1	0	0	0	0	0	0	0	1
Bombus impatiens	0	0	1	3	6	3	17	2	1	0	0	0	33
Bombus perplexus	0	0	0	0	1	0	0	0	0	0	0	0	1
Bombus sandersoni	0	0	0	0	1	0	0	0	1	0	0	0	2
Ceratina calcarata	0	3	3	12	48	32	99	35	5	1	1	0	239
Ceratina dupla	0	1	0	2	26	0	4	0	0	0	0	0	33
Ceratina mikmaqi	0	0	0	0	2	1	1	0	0	0	0	0	4
Ceratina strenua	0	0	0	2	11	0	0	0	1	2	0	0	16
Eucera atriventris	0	0	0	0	0	0	0	1	0	0	0	0	1
Habropoda laboriosa	0	0	0	8	7	0	0	0	0	1	0	0	16
Nomada bidentate_group	0	3	9	5	6	7	6	5	0	0	0	0	41
Nomada composita	0	1	0	0	0	0	0	0	0	0	0	0	1
Nomada cressonii	0	0	1	1	0	0	1	0	0	2	0	0	5
Nomada denticulata	0	0	0	2	5	3	3	0	0	0	0	0	13
Nomada depressa	1	0	0	3	4	0	0	0	0	0	0	0	8
Nomada fragariae	0	0	0	0	0	0	0	0	1	1	0	0	2

Nomada imbricata	0	1	0	2	6	12	55	17	6	1	0	0	100
Nomada lehighensis	2	2	0	0	0	0	2	0	0	0	0	0	6
Nomada luteola	0	0	0	0	1	2	1	0	0	0	0	0	4
Nomada luteoloides	0	0	4	27	78	54	38	3	3	1	0	0	208
Nomada maculata	0	0	1	0	12	13	20	3	0	0	0	0	49
Nomada pygmaea	0	0	4	8	18	23	29	3	0	1	0	0	86
Nomada sayi_illinoensis	0	0	0	0	1	3	3	1	0	0	0	0	8
Nomada sulphurata	0	0	0	4	2	4	4	0	0	0	0	0	14
Xylocopa virginica	0	0	0	0	0	0	1	0	0	0	0	0	1
Total	28	141	427	750	967	563	657	272	85	37	8	4	3939