# Native Bees (Hymenoptera: Apoidea: Anthophila) in Xeric Habitats in the Northeast U.S.

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# Abstract

In 2018, the Northeast Association of Fish and Wildlife Agencies (NEAFWA), through the Northeast Fish and Wildlife Diversity Technical Committee (NEFWDTC) and the Regional Conservation Needs Grant Program, initiated a 5-year project with the objective of improving habitat management of Barrens in the Northeastern U.S. The states funded the “Xeric Habitat for Pollinators” project due to the known concentration of Regional Species of Greatest Conservation Need at xeric sites, including rare solitary ground nesting bees associated with sandy soils. To characterize the bee community as completely as possible and maximize data consistency across sites, a protocol for bee monitoring was developed. Twenty participating sites set 120-m transects of bee bowls on 5 visits from May to October with most sites surveying from 2019-2021. Collected specimens were identified by Joan Milam in 2018 and Clare Maffei and Sam Droege in 2019-2021. Sam Droege (USGS) and Clare Maffei (USFWS) also classified species by rarity, nesting traits, and barrens associations. In total, the project dataset found 276 species from almost 20,000 collected. Based on literature and professional judgment, 32 species were identified as xeric associates, 15 of which were found to occur at project sites. In general, drier and more open sites were associated with higher bee abundance and diversity. Sandier sites had higher abundance while diversity was highest in colder sites. The Albany Pine Bush Preserve documented the greatest bee species richness (138) and Pocomoke State Forest has occurrence of the largest number of xeric associated species (8).

# Introduction

## Project Overview

In 2018, the Northeast Association of Fish and Wildlife Agencies (NEAFWA) through the Northeast Fish and Wildlife Diversity Technical Committee (NEFWDTC) initiated a 5-year project with the objective of improving habitat management of Xeric Habitats in the Northeastern U.S. The states funded the “Xeric Habitat for Pollinators” project due to the known concentration of Regional Species of Greatest Conservation Need at barrens sites. In particular, several species of rare lepidoptera were known to be obligates of barrens habitats, and several solitary ground nesting bees were understood to prefer sandy soils. The project plan incorporated four components: habitat management with vegetation, bee, and nocturnal moth surveys

Xeric ecosystems, often called barrens, have low density vegetation that was historically maintained by fire. Well-drained, nutrient poor soils underly these sites and may also be responsible for the characteristic vegetation condition. These habitats occur throughout the Midwest and eastern United States but in the Northeast they are often small in spatial extent and isolated from other similar habitats (e.g. Corbin & Flatland 2022). In part because of the limited spatial extent and low connectedness, many rare species are associated with these sites including bees and other insects (Wagner et al. 2003).

Xeric habitats are dry compared to other habitats (e.g. mesic and hydric habitats). In the Northeast U.S., xeric habitats have well-drained and sometimes deep soils comprised of sand, shale, or other rocky substrate which provide dry conditions despite occurring in humid, temperate ecosystems, sometimes near rivers, streams, or wetlands (e.g. (Sohl 2003; Quigley 2020; Corbin & Flatland 2022). Well-drained, nutrient poor soils underly these sites and may be responsible for the characteristic vegetation condition (Heikens & Robertson 1995; Petersen & Drewa 2009; Quigley 2020). Many xeric habitats are called barrens and have open canopies and a high proportion of forbs that provide good pollen and nectar sources for insects (e.g. Wagner et al. 2003, Shuey et al. 2012, Roberts et al. 2017, Walker et al. 2021, Milam et al. 2022). In the Northeast these habitats are also referred to as sandplains, sandplain grasslands, sand barrens, heathlands, scrub oak shrubland, dry woodlands, glades, shrubland barrens, pitch pine-oak woodland, and grasslands.

The vegetation communities that root in the well-drained sandy soils are adapted to frequent wildfire which historically maintained the open understory and patches of bare soil characteristic of the habitat. Common trees include scrub oak and All reports and journal articles about this habitat type describe the importance of frequent moderate to high-intensity fire, including the historical use of fire by native Americans to maintain open understories, grassy areas, and pathways (e.g. (Heikens & Robertson 1995; Wagner et al. 2003; Droege et al. 2009; Petersen & Drewa 2009; Woodside 2016). Characteristic vegetation endemic to these habitats requires natural or, in its absence, managed disturbance (Oehler et al. 2006).

Bees are an important conservation target across all habitat types due to documented declines (e.g. (Cameron et al. 2011; Bartomeus et al. 2013; Koh et al. 2016; Wagner 2020). Forest openings or gaps have been shown to have more abundant and more diverse bee communities (Roberts et al. 2017). Importantly, a recent paper found that the generally accepted trend of higher abundance of bees in open-canopy areas is not simply an artifact of not sampling in the forest canopy (Milam et al. 2022). Over the past two decades, several studies have demonstrated the importance of barrens habitats specifically for rare and diverse bee communities, as well as associated rare plant species. This has been documented in a large variety of barrens habitats including shale barrens (Latham 2020, Kalhorn et al. 2003) and pine barrens (Tucker & Rehan 2019, Bried & Dillon 2012, Winfree et al. 2007), as well as other types of xeric habitats that share many characteristics of more typical barrens communities; these include upland sand dunes (Selfridge et al. 2017), coastal beaches and islands (Burrell 2019, Zarrillo & Stoner 2019, Ascher et al. 2014, Orr 2010) and “micro-desserts” as described by Droege et al. (2009) as areas along the Patuxent River (MD) characterized by small, remnant patches of deep sand often associated with old sand mining operations. The high proportion of singleton observations in barrens surveys may also be an indication that the community has many rare species compared to other habitats (Walker et al. 2021).

Based on these studies and best professional judgment, the team identified the following as having a moderate to strong association with barrens habitats:

Table . The strength of xeric habitat association, reason for association, and references.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Family | Species | Association | Reason for barrens association | References |
| Andrenidae | *Andrena braccata* | Associated | Psammophilic, soil nesting, Dune/beach specialist | (Orr 2010; Bried & Dillon 2012) |
| Andrenidae | *Andrena carolina* | Obligate | Narrowly oligolectic - Associated with *Ericaceae,* soil nesting |  |
| Andrenidae | *Andrena fulvipennis* | Obligate | Psammophilic, nests in sandy soil | (Droege et al. 2009) |
| Andrenidae | *Andrena kalmiae* | Obligate | Oligolectic - Associated with *Ericaceae,* soil nesting |  |
| Andrenidae | *Perdita bequaerti* | Associated | Open, sandy sites, soil nesting | (Grundel et al. 2011) |
| Andrenidae | *Perdita octomaculata* | Obligate | Soil nesting | (Droege et al. 2009; Orr 2010; Grundel et al. 2011) |
| Andrenidae | *Perdita swenki* | Associated | Open, sandy sites | (Grundel et al. 2011) |
| Apidae | *Anthophora walshii* | Obligate | Nest in deep sand soil | (Cane 1991) |
| Apidae | *Melissodes dentiventris* | Obligate | Psammophilic, Associated with *Asteraceae*, soil nesting | (Goldstein & Ascher 2016) |
| Apidae | *Epeolus ainsliei* | Associated | Psammophilic | (Onuferko 2021) |
| Colletidae | *Colletes bradleyi* | Associated | Associated with blueberry | (Winfree et al. 2007) |
| Colletidae | *Colletes inaequalis* | Associated | Psammophilic (30-64% sand), soil nesting | (Arduser 2010; López-Uribe et al. 2015) |
| Colletidae | *Colletes mitchelli* | Obligate |  | (Orr 2010) |
| Colletidae | *Colletes thoracicus* | Associated | Soil nesting | (Cane 1991; Orr 2010; Grundel et al. 2011) |
| Halictidae | *Agapostemon splendens* | Associated | Psammophilic, nests in sandy soil to deep sand but doesn’t require barrens vegetative community | (Droege et al. 2009; Orr 2010; Grundel et al. 2011; Goldstein & Ascher 2016; Selfridge et al. 2017) |
| Halictidae | *Lasioglossum arantium* | Obligate | Soil nesting |  |
| Halictidae | *Lasioglossum fedorense* | Associated |  | (Grundel et al. 2011) |
| Halictidae | *Lasioglossum floridanum* | Associated | Soil nesting | Maybe (Selfridge et al. 2017) |
| Halictidae | *Lasioglossum georgeickworti* | Obligate | Soil nesting | (Zarrillo & Stoner 2019) |
| Halictidae | *Lasioglossum halophitum* | Associated | Psammophilic | (Orr 2010) |
| Halictidae | *Lasioglossum katherineae* | Associated | Psammophilic, soil nesting | (Goldstein & Ascher 2016) |
| Halictidae | *Lasioglossum lustrans* | Associated | Psammophilic, soil nesting | (Arduser 2010; Orr 2010) |
| Halictidae | *Lasioglossum marinum* | Obligate | Soil nesting | (Orr 2010; Ascher et al. 2014; Goldstein & Ascher 2016; Zarrillo & Stoner 2019) |
| Halictidae | *Lasioglossum nymphale* | Obligate | Psammophilic | (Orr 2010) |
| Halictidae | *Lasioglossum pictum* | Associated | Open, sandy sites | (Grundel et al. 2011) |
| Halictidae | *Lasioglossum raleighense* | Obligate | Oligolectic including *Fabaceae*, soil nesting |  |
| Halictidae | *Lasioglossum sopinci* | Obligate | Psammophilic, nests in deep sand | (Droege et al. 2009; Selfridge et al. 2017) |
| Halictidae | *Lasioglossum swenki* | Associated |  | (Grundel et al. 2011) |
| Halictidae | *Lasioglossum vierecki* | Obligate | Maybe nesting requirements, soil nesting | (Droege et al. 2009; Grundel et al. 2011; Bried & Dillon 2012; Goldstein & Ascher 2016) |
| Nomadinae | *Nomada electa* | Associated | Nest parasite of xeric associate (Andrena braccata) | (Bried & Dillon 2012) |
| Nomadinae | *Nomada rubicunda* | Obligate | Nest parasite of Agapostemon splendens only in deep sand |  |
| Nomadinae | *Nomada tiftonensis* | Obligate | Nest parasite of sand obligate | (Bried & Dillon 2012) |

Barrens obligate or associated bee species are likely dependent on several factors including (1) well-drained soil as a nesting substrate; (2)obligate plants as a food source for larvae and adults; and (3) active management to maintain these resources. Species identified as barrens obligates or associates have documented relationships with *Ericaceae* (heath including blueberry), *Asteraceae* (asters), *Lamiaceae* (monardas), *Ceanothus americanus* (New Jersey Tea), *Fabeaceae* (legumes) (Fowler 2016).

Though reports of ground nesting bee requirements are sparse, the importance of soil conditions for nest building, egg, larva, and pupa development, and overwintering cannot be overstated (Harmon-Threatt 2020). In her 2020 review of literature, Harmon-Threatt estimated that 83% of bees are ground nesting, but found nesting information was available for only 26% of 527 researched bee species. Factors influencing nest-site selection include abiotic factors (soil texture, soil compaction, soil moisture, temperature, and soil surface features) and biotic factors (natural enemies, presence of conspecifics, and floral and nesting resources) (Antoine & Forrest 2020). Finally, a study of nests across a range of species and geographies demonstrated a general preference of bees for sandy substrates (Cane 1991). While conclusive information about nesting requirements can only be reported by observation of bees using nest sites, the soil conditions reviewed in this paper support a correlative exploration of abiotic factors that support bee species.

## Management in Xeric Habitats

In the Northeast U.S. barrens require habitat management to maintain open canopies. Prescribed fire, canopy thinning, and mowing are common strategies (Heilferty et al. 2023). These management strategies impact bee communities directly when individuals in any life stage are present during management and indirectly when the resulting habitat condition meets life history requirements in different ways (Mitchell et al. 2022). In general, plant diversity, nesting resources, fire frequency, and habitat shading are expected to influence bee communities (Grundel et al. 2010). In the last decade, several studies have explored the impact of these habitat management activities on bee abundance and diversity.

### Fire alone

Specifically, a study of heat tolerance of bees’ four life stages found that pupal stages survived best and that 9% of the shallowest nesting mining bee species are likely to die from wildfire given know heat penetration depths (Cane & Neff 2011). Species with the shallowest nests would be most vulnerable to heating, including the horizontal nests of megachilids (Osmia and Megachile). Twig and stem cavity nesting bees are unlikely to survive prescribed fire.

A study of fire frequency and ground nesting bees found that bee abundance, richness, and diversity were higher in burned plots than unburned plots, and annual prescribed fire maximized some of these measures (Ulyshen et al. 2021). Similarly, a study in the sandhills of North Carolina investigating effects of prescribed fire found an increase in abundance and diversity of flowering plants, and a lower basal area, canopy cover, and ground cover than control plots, with increases in bee abundance and diversity (Moylett et al. 2020). Notably, a study of fire effects on bumble bees found that although prescribed fire increased floral genus richness there were no measurable effects on bumble bee community composition, species richness, or abundance (Tai et al. 2022).

### Timing of fire

Prescribed fire is commonly implemented in the winter dormant season but growing season fires can produce more bare soil and be more effective. The difference in seasonality of prescribed fire also affects bee communities differently, as bees are not mobile during winter months, although ground nesting bees may be protected from fire if nests are sufficiently deep (Cane & Neff 2011). A 2019 study of fire season and bee communities found that growing season burns produced the greatest bare ground area and increase in overall bee abundance (Decker & Harmon-Threatt 2019).

### Fire and canopy thinning

A 2014-2016 study of prescribed fire and prescribed fire and mechanical thinning in a temperate forest in North Carolina, U.S., found higher abundances and diversities of bees and other flower visitors (Campbell et al. 2018). In a midwestern fire-dependent oak ecosystem, the combination of thinning and burning increased bee abundance, richness, and Shannon’s diversity, while burning alone did not (Lettow et al. 2018). Furthermore, thinning and burning resulted in a distinct bee community, while the community in the plot with fire alone resembled the unmanaged reference plots (Lettow et al. 2018).

### Thinning alone

Regardless of land use history, canopy thinning in a longleaf pine savanna resulted in greater bee abundance and community richness (Odanaka et al. 2020). Of the five species found to have significant habitat condition preferences, three are considered xeric obligates in the Northeast US. Lasioglossum nymphale, and L. vierecki were correlated with thinned treatments, while L. raleighense was correlated with unthinned post-agricultural treatments (Odanaka et al. 2020).

### Fire and mowing

At the Ossipee Pine Barrens, New Hampshire, a one-day sampling event showed significantly higher abundance and richness in plots that were burned and mowed vs. plots that were burned, mowed, or had no management activities (Tucker & Rehan 2019).

### Herbicide and Hand Pulling

Particularly if invasive plant removal is a habitat objective, herbicide treatment and hand-pulling can be options to remove specific plants and shift the vegetation composition.

### Combination

A meta-analysis of pyroentomology literature for butterflies, bees, and ground beetles found that “across 100 studies and 445 effects, bee biodiversity increased after fire and fire in combination with forest/grassland management treatments. In contrast, fire had no significant positive or negative effect on ground beetle and butterfly biodiversity.” (Mason Jr et al. 2021)

# Field Site Description

The geographic extent of the study area in the Northeastern US comprises humid temperate ecoregions, and site conditions are influenced by differences in climate and topography. Many sites in this study are located near the coast in the Northeastern Coastal Zone, the Atlantic Coastal Pine Barrens, and the Middle Atlantic Coastal Plain (Fig. 1) (US EPA 2015). Inland from these are the sites in the Northeastern Highlands, Eastern Great Lakes Lowlands, Ridge and Valley, and Blue Ridge ecoregions.

Sites participating in this project range in size from less than 100 acres to more than 3000 acres and include grasslands, heathlands, scrub oak shrublands, and pitch pine-oak woodlands. Sites vary widely in historic land use, recent management effort, current condition, and compatibility with adjacent lands. To support statistical analysis, sites were categorized simply as grassland or woodland. Sites with little or no management in the decade leading up to this project were classified as “unmanaged” (Table 1).

Table 1. List of participating sites with key habitat characteristics including vegetation type and classification of 10-year prior management.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Site, state | Land Manager | Habitat Type | Prior Management | Data Contributed |
| EPA Level III Ecoregion: Northeastern Highlands |
| Ossipee Pine Barrens, New Hampshire | The Nature Conservancy | Woodland | Managed and Unmanaged units | Vegetation, Bee, and Moth |
| EPA Level III Ecoregion: Northeastern Coastal Zone |
| Kennebunk and Wells Barrens, Maine | The Nature Conservancy | Grassland | Managed | Vegetation, Bee, and Moth |
| Concord Pine Barrens, New Hampshire | New Hampshire Fish & Game | Woodland | Managed | Vegetation, Bee, and Moth |
| Albany Pine Bush Preserve, New York | Albany Pine Bush Preserve Commission | Woodland | Managed | Vegetation, Bee, and Moth |
| Nicholas Farm Wildlife Management Area, Rhode Island | Rhode Island Department of Environmental Management | Grassland | Unmanaged | Vegetation, Bee, and Moth |
| Pratt Farm Wildlife Management Area, Rhode Island | Rhode Island Department of Environmental Management | Woodland | Unmanaged | Vegetation, Bee, and Moth |
| EPA Level III Ecoregion: Atlantic Coastal Pine Barrens |
| Katama, Massachusetts | The Nature Conservancy | Grassland | Managed | Vegetation, Bee, and Moth |
| Linda Loring Nature Foundation, Massachusetts | Linda Loring Nature Foundation | Grassland | Unmanaged | Vegetation, Bee, and Moth |
| Head of the Plains, Nantucket, Massachusetts | Nantucket Conservation Foundation | Grassland | Managed | Vegetation, Bee, and Moth |
| Warren Grove, New Jersey | NJ Dep’t of Environmental Protection Fish and Wildlife | Woodland | Managed and Unmanaged units | Vegetation, Bee, and Moth |
| EPA Level III Ecoregion: Ridge and Valley |
| Scotia Barrens, Pennsylvania | PA Game Commission and Patton Township | Woodland / Grassland | Managed | Vegetation, Bee, and Moth |
| Sideling Hill, Pennsylvania | Western Pennsylvania Conservancy | Woodland | Unmanaged | Vegetation, Bee, and Moth |
| Green Ridge State Forest, Maryland | Maryland Dep’t of Natural Resources | Grassland | Managed | Vegetation, Bee, and Moth |
| EPA Level III Ecoregion: Blue Ridge |
| Michaux State Forest, Pennsylvania | Pennsylvania Dep’t of Conservation & Natural Resources | Woodland | Managed and Unmanaged units | Vegetation, Bee, and Moth |
| EPA Level III Ecoregion: Eastern Great Lakes Lowlands |
| Presque Isle State Park, Pennsylvania | Pennsylvania Dep’t of Conservation & Natural Resources | Grassland | Unmanaged | Bee |
| Sandbar Wildlife Management Area, Vermont | Vermont Fish & Wildlife Department | Grassland | Managed | Bee |
| EPA Level III Ecoregion: Middle Atlantic Coastal Plain |
| Nanticoke Wildlife Area, Delaware | Delaware Dep’t of Natural Resources and Environmental Control | Woodland | Unmanaged | Vegetation, Bee, and Moth |
| Pocomoke State Forest, Maryland | Maryland Dep’t of Natural Resources | Woodland | Managed | Vegetation, Bee, and Moth |

Most sites involved in this project have soils with sand fraction greater than 70%, though sites in the Ridge and Valley province have lower sand fractions (25-55%). More than 75% of sites have less than 10% organic matter, as is expected in barrens, but some exceptions include Nicholas and Pratt Farms in Rhode Island which have >16% organic matter. Barrens are often characterized as having low soil fertility (e.g. (Quigley 2020). Effective cation exchange coefficients (ECEC) ranged from 1 to 10 meq/100g at sites participating in this study, and sites with over 75% sand had less than 6 meq/100g ECEC. Bulk Density ranged from 1.03 to 1.54 g/cm3 with an inverse relationship to soil organic matter.

# Methods

We proposed two complementary methods to sample bees, pan-trapping using bee bowls and timed target-netting. Sampling protocols used for the study are loosely based on those put forth by (LeBuhn et al. 2003) and adapted from the Very Handy Bee Manual (Droege 2015). Ideally, both sampling methods would be utilized as they each capture a different and complementary community of bees (Wilson et al. 2008). However, due to lack of staff and difficulty in training surveyors, most sites only completed pan-trapping. Sampling was conducted once each in five two-week windows between May and September (May 1-May 14, June 3-June 17, July 1- July 23, August 5- August 19, and September 10- September 24) from 2019 to 2022. In order to standardize for hymenopteran activity, sites aimed to sample only on calm sunny days (>90% sun) with air temperatures above 20°C. These conditions maximize activity of bees, as they are generally not active under cool or rainy conditions and only forage once they have sufficiently warmed up (Roberts & Harrison 1998).

The number of transects per site was determined by planned management activities in management units and staff capacity. Some sites began monitoring in 2018 to test the protocol, while others joined the project in 2020.

Table . Number of transects and total number of sampling dates for all transects at participating sites.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| State | Site | Number of Transects | Complete Sampling Years\* | Total Number of Sampling Dates |
| Maine | Wells Barrens | 1 | 2 | 9 |
| Maine | Kennebunk Plains | 1 | 2 | 8 |
| New Hampshire | Concord Pine Barrens | 3 | 1 | 24 |
| New Hampshire | Ossipee Pine Barrens | 1 | 4 | 14 |
| Vermont | Sandbar Wildlife Management Area | 1 | 4 | 18 |
| Massachusetts | Head of the Plains | 3 | 4 | 57 |
| Massachusetts | Linda Loring Nature Foundation | 2 | 4 | 37 |
| Massachusetts | Katama Airfield and The Farm | 2 | 4 | 24 |
| Rhode Island | Pratt Farm | 2 |  | 7 |
| Rhode Island | Nicholas Farm | 2 | 1 | 7 |
| New York | Albany Pine Bush Preserve | 5 | 3 | 75 |
| Pennsylvania | Presque Isle | 4 | 2 | 39 |
| Pennsylvania | Sideling Hill | 3 | 2 | 27 |
| Pennsylvania | Scotia Barrens | 3 | 2 | 33 |
| Pennsylvania | Michaux State Forest | 3 | 2 | 30 |
| New Jersey | Warren Grove | 3 | 1 | 22 |
| Maryland | Pocomoke | 2 | 4 | 29 |
| Maryland  | Green Ridge State Forest | 1 | 3 | 11 |
| Delaware | Nanticoke Wildlife Area | 2 | 2 | 7 |

\*site ran all transects at least 3 out of 5 sampling windows in a given year

For pan-trapping, plastic souffle cups painted with blue, yellow, and white ultraviolet paints were filled at least halfway with water and non-citrus detergent. The color of the bowls is attractive to the bees while the soap breaks the surface tension of the water allowing for the lethal capture of bee specimens. The bee bowls were laid out in transects consisting of 24 bowls placed 5-10 meters apart and alternating between the colors. The start and end points of the transects were permanently marked in the field or with a GPS unit so that the same transect could be monitored over the course of the season and from year to year. Transects were situated so they were at least 30 meters away from habitat edges. Pan traps were either placed before 9:00 am and removed by 5:00 pm the same day or alternatively put in place after 5:00 pm the day before and left out for no more than 24 hours. All captured specimens at a site were then pooled, strained, and placed in labeled whirl-pak bags with 70% ethanol.

It should be noted, pan traps are not specific to bees and catch a wide variety of insects including flies, butterflies, moths, wasps, beetles, etc. Some sites in the project have rare or protected insects (i.e., Frosted elfin, Karner blue), and did not use pan traps during the flight periods of these animals unless they had permissions/permits from the appropriate agencies.

Timed target-netting was conducted on the same days as pan-trapping at a subset of sites that had the ability. This method involved walking through the site with a standard insect net and catching every bee or bee-like insect seen in a 30-minute time period. Netting took place during peak bee activity from 10:00-14:00; however, this time window was extended to 9:00-16:00 if days were warm, especially later in the season. Surveyors aimed to stay within 10 meters of the pan-trap transect line and netted insects from vegetation, the ground or in-flight. Everything that looked like a bee was captured and placed into a vial containing 70% ethanol. The time was paused while specimens were being transferred from the net to the ethanol. Net samples were then transferred to whirl-pak bags for storage and transport.

During netting and/or pan-trapping surveyors recorded weather conditions (temperature, wind speed, and cloud cover), as well as the top five most abundance plants in bloom. For pan-trapping, the date and time of bowl deployment and retrieval were also recorded as well as the number of bowls that contained specimens (some would inevitably be tipped over or leak). For netting, the start and end time of the 30-minute netting period was recorded.

In 2018 all specimens were mailed to Joan Milam at the University of Massachusetts for identification. In 2019-2022, all specimens were mailed to the USGS Native Bee Inventory and Monitoring Lab at the Patuxent Wildlife Research Center in Laurel, Maryland. There, Sam Droege, Clare Maffei, and Sydney Shumar sorted, pinned, and identified the specimens to the species level when possible.

To better understand the role soil plays at project study sites, we used data from the Soil Survey Geographic Database (SSURGO) and measured soil crusting at sites. We selected soil characteristics based on knowledge of barrens site characteristics and review papers exploring bee nest site suitability (Antoine & Forrest 2020). We selected the following soil characteristics to understand site similarities and differences, particularly as may affect bee communities:

* Number of frost-free days (a proxy for latitudinal and coastal climate gradients)
* Organic matter, sand, silt, and clay percentages in the A horizon
* Annual minimum water table depth
* Bulk Density
* Effective Cation Exchange Capacity
* pH

To establish the context of the xeric habitat bee community results from this study, we used the North American Bee Distribution Tool (NABDT), extracting observations for the ten states represented by our project (Weaver 2020). This extract, from Maine, New Hampshire, Vermont, Massachusetts, New York, Rhode Island, New Jersey, Pennsylvania, Maryland, and Delaware on October 31, 2022, yielded 427,517 records of 699 bees.

## Analysis Methods

Please see the project’s sister publication for complete statistical analysis and results (Barton & Poulos 2023).

# Results

In total, sites ran 46 bee bowl transects on 602 dates in 2018 through 2021, with a limited effort in sweep netting, and collected 23529 bee specimens representing 273 species. In the 9-state region represented by this study, there are at least 699 bee species (Weaver 2020), of which 271 were detected in this project (Appendix A).

In general, drier and more open sites were associated with higher bee abundance and diversity. Sandier sites had higher abundance while diversity was highest in colder sites. Albany Pine Bush Preserve (5 transects 3 years), Sandbar Wildlife Management Area (1 transect 4 years), and the Scotia Barrens (3 transects 2 years) documented the largest number of species (Fig. 1). Species richness, when measured as an average number of species collected per transect, was highest in Sandbar Wildlife Management Area and Albany Pine Bush Preserve (Fig. 2).

Figure . Species richness detected at participating sites. Data are not corrected for differences in sampling effort.

Figure . Left: mean species richness per transect by site, Right: Multiple comparisons among sites of number of species showing means and 1 SE (black dot and purple bars). Two sites are significantly different if their red arrows do not overlap.



Figure . Non-metric multidimensional scaling (NMDS) for 39 bee transects showing differences in species composition among ecoregions along the first two axes. Ellipses show 95% confidence interval for each ecoregion. Non-overlapping ellipses signify large differences between ecoregions. Colors of ellipses match those of ecoregion names.

Bee communities were significantly different across sites and ecoregions (Fig. 3). These differences in bee species community are attributed in part to indicator species that occurred significantly more often in grassland sites compared to woodland sites (Table 3) or in each ecoregion (Table 4) or in specific sites (Table 5). These lists show bee species that occur statistically significantly more often in the identified area.

Table . Indicator species analysis of NMDS bee species composition by vegetation type.

|  |  |  |  |
| --- | --- | --- | --- |
| **GRASSLAND** | **Statistic** | **WOODLAND** | **Statistic** |
| Augochlorella.aurata | 0.882\*\* | Lasioglossum.subviridatum | 0.566\* |
| Agapostemon.virescens | 0.843\*\*\* | Sphecodes.mandibularis | 0.551\* |
| Lasioglossum.oceanicum | 0.707\*\* |  |  |
| Megachile.brevis | 0.7\*\*\* |  |  |
| Andrena.carlini | 0.685\*\* |  |  |
| Lasioglossum.acuminatum | 0.667\* |  |  |
| Nomada.articulata | 0.593\* |  |  |
| Lasioglossum.zonulum | 0.527\* |  |  |
| Nomada.denticulata | 0.471\* |  |  |

Table . Indicator species analysis of NMDS of bee species composition by ecoregion.

|  |  |
| --- | --- |
| **ATLANTIC COASTAL PINE BARRENS** | **Statistic** |
| Lasioglossum.oceanicum | 0.864\* |
| Megachile.brevis | 0.841\* |
| **BLUE RIDGE** |  |
| Augochlora.pura | 0.84\* |
| **EASTERN GREAT LAKES LOWLANDS** |  |
| Agapostemon.splendens | 0.885\* |
| Lasioglossum.zonulum | 0.882\* |
| Lasioglossum.oblongum | 0.842\* |
| **NORTHEASTERN HIGHLANDS** |  |
| Lasioglossum.fattigi | 1\* |
| Lasioglossum.taylorae | 0.877\* |

Table . Indicator species analysis of NMDS bee species composition by site.

|  |  |
| --- | --- |
| **ALBANY PINE BUSH** | **Statistic** |
| Lasioglossum.vierecki | 0.984\*\* |
| **HEAD OF PLAINS** |  |
| Megachile.addenda | 1\* |
| **LINDA LORING** |  |
| Lasioglossum.fuscipenne | 1\* |
| **PRESQUE ISLE** |  |
| Agapostemon.splendens | 0.984\* |
| Lasioglossum.zonulum | 0.953\* |
| **WARREN GROVE** |  |
| Lasioglossum.arantium | 1\* |
| Lasioglossum.sopinci | 1\* |

## Management Treatments

There was no detectable effect, positive or negative, of active management on bee abundance or diversity. There were also no significant differences in sites with a decade of prior management compared with newly managed sites, and no differences between sites surrounded by similar habitat vs. isolated sites. However, sites with long-term management and higher quality habitat had higher bee species diversity.

## Xeric Obligate Bees

Based on available data and experience, we identified 32 species that are expected to be associated with or obligate to barrens habitats (Table 1). Fifteen of these xeric associates were found at sites (Table 6). Pocomoke State Forest in Maryland collected the highest diversity of xeric associated bees (8 species) and it is the only site where *Lasioglossum lustrans* was collected. Albany Pine Bush Preserve in New York collected 6 xeric associated species including the largest collection of *L. vierecki*.

Table . Abundance of xeric associated species occuring at sites.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Family | Name | Grand Total | Kennebunk Plains | Wells Barrens Preserve | Concord Pine Barrens | Sandbar Wildlife Management Area | Head of Plains | Katama Airfield | Linda Loring Nature Foundation | Albany Pine Bush Preserve | Michaux State Forest | Presque Isle | Sideling Hill | Warren Grove | Green Ridge State Forest | Pocomoke State Forest | Nanticoke Wildlife Area |
| Andrenidae | Andrena braccata | 1 |  |  |  |  |  |  | 1 |  |  |  |  |  |  |  |  |
| Andrena carolina | 4 |  |  |  |  | 1 |  |  |  | 3 |  |  |  |  |  |  |
| Perdita octomaculata | 28 |  |  |  |  |  |  |  | 25 |  | 1 |  |  |  | 2 |  |
| Colletidae | Colletes inaequalis | 16 |  |  |  | 2 |  |  |  | 14 |  |  |  |  |  |  |  |
| Colletes thoracicus | 12 |  |  |  |  |  |  | 1 | 1 |  | 3 |  |  |  | 1 | 6 |
| Halictidae | Agapostemon splendens | 374 |  |  |  |  |  |  |  | 21 |  | 342 |  |  |  | 11 |  |
| Lasioglossum arantium | 40 |  |  |  |  |  |  |  |  |  |  |  | 36 |  | 4 |  |
| Lasioglossum floridanum | 123 |  |  | 1 |  |  |  |  |  |  |  |  |  |  | 122 |  |
| Lasioglossum georgeickworti | 9 |  |  |  |  | 7 |  | 1 |  |  |  |  |  | 1 |  |  |
| Lasioglossum katherineae | 46 | 8 | 27 | 6 |  |  |  |  | 1 |  | 1 | 3 |  |  |  |  |
| Lasioglossum lustrans | 2 |  |  |  |  |  |  |  |  |  |  |  |  |  | 2 |  |
| Lasioglossum marinum | 8 |  |  |  |  |  |  | 8 |  |  |  |  |  |  |  |  |
| Lasioglossum nymphale | 26 |  |  |  |  |  |  |  |  |  |  |  | 26 |  |  |  |
| Lasioglossum sopinci | 39 |  |  |  |  |  |  |  |  |  |  |  | 38 |  | 1 |  |
| Lasioglossum vierecki | 460 |  |  |  | 30 |  | 3 |  | 385 |  |  |  |  |  | 42 |  |
|  | Grand Total | 1188 | 8 | 27 | 7 | 32 | 8 | 2 | 11 | 447 | 3 | 347 | 3 | 100 | 1 | 185 | 6 |

Bees that were expected to be barrens obligates (Table 1) but were not found in our collection include *Andrena fulvipennis, Andrena kalmiae, Anthophora walshii, Colletes bradleyi, Colletes mitchelli, Epeolus ainsliei, Lasioglossum fedorense, Lasioglossum halophitum, Lasioglossum pictum, Lasioglossum raleighense, Lasioglossum swenki, Melissodes dentiventris, Nomada electa, Nomada rubicunda, Nomada tiftonensis, Perdita bequaerti,* and *Perdita swenki*.

In general, common bees found at most sites had higher total abundance in the dataset (Fig. 4). *Augochlorella aurata* was the only species collected at all 20 sites with the largest total number of specimens (7,849). Some species, though collected at only one or two sites, had high abundance – *Lasioglossum vierecki* was represented strongly in surveys at three sites and *Agapostemon splendens* had a large collection at Presque Isle. Twenty species identified as rare bees based on existing datasets were found (Table 7)*. Lasioglossum arantium* and *L. sopinci* were each found at two sites with 40 and 39 specimens each. *L. katherinae* was found at 6 sites with a total of 46 specimens. *Andrena regularis* was found at 2 sites with a total of 21 specimens. All other rare species were found with just 1-4 specimens at a few sites.



Figure . Number of specimens collected (total) by number of sites where the species was observed.

Table . Rare bees collected.

|  |  |  |  |
| --- | --- | --- | --- |
|  |  |  | Total collected |
| Family | Subfamily | Scientific Name |
| Grand Total | **184** |
| Andrenidae | Andreninae | Andrena braccata | 1 |
| Andrena regularis | 21 |
| Panurginae | Perdita bradleyi | 3 |
| Protandrena abdominalis | 2 |
| Apidae | Nomadinae | Nomada armatella | 4 |
| Nomada bethunei | 1 |
| Nomada obliterata | 1 |
| Nomada valida | 2 |
| Colletidae | Colletinae | Colletes solidaginis | 6 |
| Hylaeinae | Hylaeus pictipes | 1 |
| Halictidae | Halictinae | Lasioglossum arantium | 40 |
| Lasioglossum katherineae | 46 |
| Lasioglossum michiganense | 1 |
| Lasioglossum sopinci | 39 |
| Sphecodes carolinus | 1 |
| Sphecodes galerus | 1 |
| Sphecodes pimpinellae | 6 |
| Megachilidae | Megachilinae | Coelioxys immaculata | 1 |
| Megachile frugalis | 3 |
| Osmia sandhouseae | 4 |

# Discussion

The sampling protocol called for pan traps (also referred to as bee bowls) and hand-netting to address sampling biases. For example, large-bodied bees like bumble bees can escape pan traps. Unfortunately, sites were staffed by people with a range of levels of experience with bee collection and with different responsibilities and time constraints at the sites. In just the first year it became evident that inexperienced surveyors were focusing on the larger bodied bees that are more recognizable and bees that were actively foraging while missing faster small bees or parasitic bees flying low to the ground. For example, in 2019, 226 Bombus sp. were netted while only 22 were caught in pan traps. Therefore, because of the inconsistent expertise and effort in hand-netting, the project was forced to rely on pan traps for statistical analysis. Concurrent with this project, a number of publications critiqued the use of pan traps for bee surveys (Embry 2020; Prendergast 2020; Portman et al. 2020). Nonetheless, given the large geographic scale and number of inexperienced personnel involved in this project, transects of bee bowls provided a consistent assessment of the bee community.

Staffing constraints also meant that over half the sites were only able to deploy one or two transects. This limited the statistical analysis of management impacts. However, if all twenty sites had run 3 or more transects each, the project may instead have been limited by the capacity of the bee identification services.

The protocol called for sampling monthly from May to September. This was the greatest frequency and duration possible given our staffing constraints but resulted in a likelihood of detecting early spring or fall bees and bees with short flight periods. Some sites did not sample in May out of an abundance of caution against inadvertent taking Frosted Elfin butterflies or because summer staff had not yet arrived at the site.

The Albany Pine Bush Preserve has a strong bee community by any measure. The site also has a large spatial extent and a long-term management dedicated to rotational management resulting in a mosaic of diverse habitat conditions and values. In short, the Albany Pine Bush has been following all of the best practices for more than a decade (Heilferty et al. 2023). Although the Albany Pine Bush Preserve is technically mapped in the Northeastern Coastal Zone, staff believe it should be mapped with Presque Isle State Park and Sandbar Wildlife Management Area in the Eastern Great Lakes Lowlands. Presque Isle and Sandbar are two sites that also have diverse and abundance bee communities.

Although bee community data did not demonstrate significant differences resulting from management during this project, long-term management did moderately enhance species diversity. The Albany Pine Bush Preserve is one example. Continued survey at sites with active management would be necessary to evaluate the response of the bee community to restoration of xeric habitat conditions.

Seventeen species that were expected to be xeric associates were not observed in this study (Table 6). Species with adult phases in the shoulder seasons of early spring or fall may have been missed by the sampling windows in this study. Species with few continental records are noted as “Rare”. Some species are more common in the Midwest or Southeast, and the Northeast represents a disjunct population.

Table . Xeric associated species not observed in this study with traits.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Species | Flight period | Feeding behavior | Nesting | Parasitic Relationship | Notes |
| *Andrena fulvipennis* | Sept-Oct | Oligolectic | Soil | Host to: Nomada |  |
| *Andrena kalmiae* | Spring | Oligolectic | Soil | Host to: Nomada |  |
| *Anthophora walshii* | Summer | Generalist | Soil |  | Disjunct in the Northeast |
| *Colletes bradleyi* |  |  |  |  | Rare |
| *Colletes mitchelli* |  |  |  |  | Rare |
| *Epeolus ainsliei* | Summer |  |  |  | Rare |
| *Lasioglossum fedorense* |  |  |  |  | Rare |
| *Lasioglossum halophitum* | Apr-Nov |  |  |  | Delmarva Peninsula |
| *Lasioglossum pictum* | Apr-Nov | Generalist | Soil |  | Disjunct in the Northeast |
| *Lasioglossum raleighense* | May-Sept | Oligolectic | Soil |  | Rare |
| *Lasioglossum swenki* | Apr-Aug | Generalist | Soil |  | Rare |
| *Melissodes dentiventris* | Jun-Nov | Oligolectic | Soil |  |  |
| *Nomada electa* | Fall |  |  | Parasite of Andrena | Rare |
| *Nomada rubicunda* | Spring | Generalist |  | Parasite of Andrena | Rare |
| *Nomada tiftonensis* | Summer |  |  | Parasite | Rare |
| *Perdita bequaerti* | Summer | Oligolectic | Soil |  |  |
| *Perdita swenki* | Aug-Sept |  |  |  | Disjunct in the Northeast |

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# Appendix A: Species List

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Family | Subfamily | Name | Grand Total | DE | ME | MD | MA | NH | NJ | NY | PA | RI | VT |
| Grand Total |  |  | 21508 | 50 | 634 | 812 | 8594 | 245 | 279 | 5633 | 2997 | 45 | 2219 |
| Andrenidae | Andreninae | *Andrena algida* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Andrena alleghaniensis* | 2 |  |  |  |  |  |  | 2 |  |  |  |
|  |  | *Andrena asteris* | 1 |  |  |  |  |  |  | 1 |  |  |  |
|  |  | *Andrena atlantica* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Andrena barbilabris* | 4 |  |  |  |  |  |  | 2 |  |  | 2 |
|  |  | *Andrena bisalicis* | 1 |  |  |  |  |  |  |  |  |  | 1 |
|  |  | *Andrena braccata* | 1 |  |  |  | 1 |  |  |  |  |  |  |
|  |  | *Andrena bradleyi* | 3 |  |  |  |  |  |  | 2 | 1 |  |  |
|  |  | *Andrena brevipalpis* | 2 |  |  |  |  |  |  | 2 |  |  |  |
|  |  | *Andrena canadensis* | 3 |  |  |  |  |  |  | 3 |  |  |  |
|  |  | *Andrena carlini* | 128 |  | 9 | 3 | 49 | 13 |  | 5 | 33 | 1 | 15 |
|  |  | *Andrena carolina* | 4 |  |  |  | 1 |  |  |  | 3 |  |  |
|  |  | *Andrena ceanothi* | 20 |  | 1 |  |  |  |  | 17 |  |  | 2 |
|  |  | *Andrena crataegi* | 75 |  | 1 |  | 1 |  |  | 65 | 2 |  | 6 |
|  |  | *Andrena cressonii* | 8 |  |  | 3 | 1 |  |  |  | 2 |  | 2 |
|  |  | *Andrena distans* | 1 |  |  |  |  |  |  | 1 |  |  |  |
|  |  | *Andrena erigeniae* | 15 |  |  |  |  |  |  |  | 15 |  |  |
|  |  | *Andrena erythrogaster* | 2 |  |  |  |  |  |  |  |  |  | 2 |
|  |  | *Andrena fragilis* | 3 |  |  |  |  |  |  |  |  |  | 3 |
|  |  | *Andrena gardineri* | 1 |  |  |  |  |  |  |  | 1 |  |  |
|  |  | *Andrena hippotes* | 1 |  |  |  |  |  |  |  |  |  | 1 |
|  |  | *Andrena hirticincta* | 6 |  |  |  |  | 1 |  | 5 |  |  |  |
|  |  | *Andrena imitatrix* | 1 |  |  |  |  |  |  |  |  |  | 1 |
|  |  | *Andrena integra* | 2 |  |  |  |  |  |  |  |  |  | 2 |
|  |  | *Andrena mandibularis* | 1 |  |  |  |  |  |  |  | 1 |  |  |
|  |  | *Andrena melanochroa* | 2 |  |  |  |  |  |  | 1 |  |  | 1 |
|  |  | *Andrena miranda* | 21 |  |  |  |  |  |  | 21 |  |  |  |
|  |  | *Andrena miserabilis* | 5 |  |  |  |  |  |  | 2 | 3 |  |  |
|  |  | *Andrena nasonii* | 56 |  |  | 5 | 31 |  |  | 8 | 10 |  | 2 |
|  |  | *Andrena nivalis* | 3 |  |  |  |  | 1 |  | 1 |  |  | 1 |
|  |  | *Andrena nubecula* | 3 |  |  |  |  |  |  | 2 | 1 |  |  |
|  |  | *Andrena nuda* | 2 |  |  |  |  |  |  |  | 2 |  |  |
|  |  | *Andrena perplexa* | 7 |  |  |  | 1 |  |  | 1 |  |  | 5 |
|  |  | *Andrena placata* | 7 |  |  |  |  |  |  | 7 |  |  |  |
|  |  | *Andrena pruni* | 4 |  |  |  |  |  |  |  | 4 |  |  |
|  |  | *Andrena regularis* | 21 |  |  |  |  | 2 |  | 19 |  |  |  |
|  |  | *Andrena robertsonii* | 1 |  |  |  |  |  |  |  |  |  | 1 |
|  |  | *Andrena rugosa* | 1 |  |  |  |  |  |  |  | 1 |  |  |
|  |  | *Andrena sigmundi* | 2 |  |  |  |  |  |  |  | 2 |  |  |
|  |  | *Andrena simplex* | 3 |  |  |  |  |  |  | 3 |  |  |  |
|  |  | *Andrena vicina* | 156 |  | 18 |  | 5 |  |  | 104 | 6 |  | 23 |
|  |  | *Andrena violae* | 3 |  |  | 1 |  |  |  |  | 2 |  |  |
|  |  | *Andrena wheeleri* | 1 |  |  |  |  |  |  |  | 1 |  |  |
|  |  | *Andrena wilkella* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Andrena ziziaeformis* | 27 |  |  |  | 8 |  |  |  | 19 |  |  |
|  | Panurginae | *Calliopsis andreniformis* | 114 |  | 1 | 9 | 12 | 1 |  | 17 | 73 |  | 1 |
|  |  | *Panurginus potentillae* | 1 |  |  |  |  |  |  |  | 1 |  |  |
|  |  | *Perdita boltoniae* | 2 | 1 |  | 1 |  |  |  |  |  |  |  |
|  |  | *Perdita bradleyi* | 3 |  |  | 3 |  |  |  |  |  |  |  |
|  |  | *Perdita halictoides* | 1 |  |  |  |  |  |  |  |  |  | 1 |
|  |  | *Perdita octomaculata* | 28 |  |  | 2 |  |  |  | 25 | 1 |  |  |
|  |  | *Protandrena abdominalis* | 2 | 2 |  |  |  |  |  |  |  |  |  |
|  |  | *Pseudopanurgus andrenoides* | 2 |  |  |  |  |  |  | 2 |  |  |  |
|  |  | *Pseudopanurgus labrosiformis* | 1 |  |  |  |  |  |  | 1 |  |  |  |
|  |  | *Pseudopanurgus solidaginis* | 1 |  |  |  |  |  |  | 1 |  |  |  |
| Apidae | Apinae | *Anthophora abrupta* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Anthophora terminalis* | 4 |  |  |  |  |  |  | 3 |  |  | 1 |
|  |  | *Apis mellifera* | 126 | 1 | 2 | 4 | 47 | 4 | 28 |  | 27 | 4 | 9 |
|  |  | *Bombus bimaculatus* | 108 |  | 17 | 4 | 29 | 4 | 1 | 4 | 38 | 1 | 10 |
|  |  | *Bombus borealis* | 1 |  |  |  |  |  |  |  |  |  | 1 |
|  |  | *Bombus citrinus* | 1 |  |  |  | 1 |  |  |  |  |  |  |
|  |  | *Bombus fernaldae* | 1 |  |  |  |  |  |  |  | 1 |  |  |
|  |  | *Bombus fervidus* | 4 |  |  | 1 |  |  |  |  | 3 |  |  |
|  |  | *Bombus griseocollis* | 132 | 1 | 12 | 13 | 25 |  | 4 | 17 | 10 |  | 50 |
|  |  | *Bombus impatiens* | 622 | 1 | 25 | 19 | 43 | 27 |  | 383 | 96 | 2 | 26 |
|  |  | *Bombus pensylvanicus* | 2 | 1 |  | 1 |  |  |  |  |  |  |  |
|  |  | *Bombus perplexus* | 35 |  |  |  |  |  | 2 |  | 32 | 1 |  |
|  |  | *Bombus rufocinctus* | 1 |  |  |  |  |  |  |  |  |  | 1 |
|  |  | *Bombus sandersoni* | 13 |  |  |  |  |  |  |  | 13 |  |  |
|  |  | *Bombus ternarius* | 3 |  |  |  |  |  |  |  |  |  | 3 |
|  |  | *Bombus terricola* | 1 |  |  |  |  |  |  |  | 1 |  |  |
|  |  | *Bombus vagans* | 23 |  |  | 2 |  | 2 | 1 |  | 18 |  |  |
|  |  | *Habropoda laboriosa* | 9 | 1 |  | 7 |  |  | 1 |  |  |  |  |
|  |  | *Melissodes apicatus* | 4 | 4 |  |  |  |  |  |  |  |  |  |
|  |  | *Melissodes bimaculatus* | 4 |  |  |  |  |  |  | 3 |  | 1 |  |
|  |  | *Melissodes comptoides* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Melissodes denticulatus* | 1 |  | 1 |  |  |  |  |  |  |  |  |
|  |  | *Melissodes desponsus* | 11 |  |  | 1 |  |  |  |  | 10 |  |  |
|  |  | *Melissodes druriellus* | 11 |  | 3 |  | 3 | 1 |  | 4 |  |  |  |
|  |  | *Melissodes illatus* | 1 |  |  |  |  |  |  | 1 |  |  |  |
|  |  | *Melissodes subillatus* | 3 |  | 1 |  |  |  |  |  | 2 |  |  |
|  |  | *Melissodes trinodis* | 2 |  |  |  | 2 |  |  |  |  |  |  |
|  |  | *Peponapis pruinosa* | 3 |  |  | 1 | 1 |  |  | 1 |  |  |  |
|  |  | *Ptilothrix bombiformis* | 1 |  |  |  |  |  |  |  |  | 1 |  |
|  | Nomadinae | *Epeolus bifasciatus* | 1 |  |  |  |  |  |  |  |  |  | 1 |
|  |  | *Epeolus pusillus* | 1 |  |  |  | 1 |  |  |  |  |  |  |
|  |  | *Epeolus scutellaris* | 5 |  |  |  | 2 |  |  | 1 | 2 |  |  |
|  |  | *Nomada armatella* | 4 |  |  |  |  |  |  | 4 |  |  |  |
|  |  | *Nomada articulata* | 26 |  |  | 1 | 7 | 1 |  |  | 2 |  | 15 |
|  |  | *Nomada australis* | 1 |  |  |  | 1 |  |  |  |  |  |  |
|  |  | *Nomada bethunei* | 1 |  |  |  |  |  |  |  |  |  | 1 |
|  |  | *Nomada bidentate\_group* | 101 |  |  |  | 1 |  |  | 78 | 5 |  | 17 |
|  |  | *Nomada cressonii* | 19 |  | 6 |  | 1 |  |  | 4 | 1 | 2 | 5 |
|  |  | *Nomada denticulata* | 7 |  | 3 |  | 1 |  |  |  | 1 |  | 2 |
|  |  | *Nomada depressa* | 1 |  |  |  |  |  |  | 1 |  |  |  |
|  |  | *Nomada gracilis* | 1 |  |  |  |  |  |  | 1 |  |  |  |
|  |  | *Nomada illinoensis* | 2 |  |  | 2 |  |  |  |  |  |  |  |
|  |  | *Nomada imbricata* | 8 |  |  |  |  | 1 |  | 1 | 3 |  | 3 |
|  |  | *Nomada lehighensis* | 1 |  |  |  | 1 |  |  |  |  |  |  |
|  |  | *Nomada luteoloides* | 4 |  | 1 |  |  |  |  | 1 | 2 |  |  |
|  |  | *Nomada maculata* | 15 |  |  |  | 2 | 5 | 1 |  | 1 |  | 6 |
|  |  | *Nomada obliterata* | 1 |  |  |  |  |  |  |  |  |  | 1 |
|  |  | *Nomada pygmaea* | 15 |  |  |  | 2 | 1 |  | 6 | 6 |  |  |
|  |  | *Nomada valida* | 2 |  |  | 2 |  |  |  |  |  |  |  |
|  |  | *Triepeolus donatus* | 1 |  |  |  |  |  |  |  | 1 |  |  |
|  | Xylocopinae | *Ceratina calcarata* | 427 | 2 |  | 16 | 14 | 2 |  | 169 | 174 |  | 50 |
|  |  | *Ceratina dupla* | 552 |  |  | 11 | 18 | 1 |  | 205 | 87 |  | 230 |
|  |  | *Ceratina mikmaqi* | 743 |  | 2 | 29 | 35 | 3 |  | 354 | 182 | 1 | 137 |
|  |  | *Ceratina strenua* | 1800 | 2 |  | 3 |  |  |  | 1533 | 260 |  | 2 |
|  |  | *Xylocopa virginica* | 52 | 3 | 1 | 1 | 4 | 2 | 1 | 34 | 2 |  | 4 |
| Colletidae | Colletinae | *Colletes americanus* | 12 |  |  |  | 4 |  |  | 2 | 6 |  |  |
|  |  | *Colletes compactus* | 3 |  |  |  |  |  |  | 1 | 2 |  |  |
|  |  | *Colletes inaequalis* | 16 |  |  |  |  |  |  | 14 |  |  | 2 |
|  |  | *Colletes mandibularis* | 3 |  |  |  | 2 |  |  |  |  |  | 1 |
|  |  | *Colletes simulans* | 15 |  |  |  | 6 |  |  | 7 | 1 |  | 1 |
|  |  | *Colletes solidaginis* | 6 |  |  | 3 | 2 |  |  |  | 1 |  |  |
|  |  | *Colletes thoracicus* | 12 | 6 |  | 1 | 1 |  |  | 1 | 3 |  |  |
|  |  | *Colletes validus* | 20 |  |  | 1 | 14 |  |  | 5 |  |  |  |
|  | Hylaeinae | *Hylaeus affinis* | 56 |  |  |  | 11 |  |  | 10 |  |  | 35 |
|  |  | *Hylaeus annulatus* | 1 |  |  |  |  |  |  | 1 |  |  |  |
|  |  | *Hylaeus illinoisensis* | 4 |  |  |  |  |  |  | 4 |  |  |  |
|  |  | *Hylaeus mesillae* | 130 |  |  |  | 23 |  |  | 39 | 17 |  | 51 |
|  |  | *Hylaeus modestus* | 20 |  |  |  | 2 | 1 |  | 6 | 7 |  | 4 |
|  |  | *Hylaeus nelumbonis* | 1 |  |  |  |  |  |  |  | 1 |  |  |
|  |  | *Hylaeus ornatus* | 5 |  |  |  |  |  |  |  |  |  | 5 |
|  |  | *Hylaeus pictipes* | 1 |  |  |  |  |  |  | 1 |  |  |  |
| Halictidae | Halictinae | *Agapostemon sericeus* | 27 |  |  |  | 2 | 1 |  | 19 | 1 |  | 4 |
|  |  | *Agapostemon splendens* | 374 |  |  | 11 |  |  |  | 21 | 342 |  |  |
|  |  | *Agapostemon texanus* | 583 |  | 79 | 2 | 145 | 7 |  | 331 | 15 | 2 | 2 |
|  |  | *Agapostemon virescens* | 529 | 1 | 12 | 4 | 435 | 13 |  | 9 | 10 | 1 | 44 |
|  |  | *Augochlora pura* | 129 | 1 |  | 13 | 1 | 1 |  | 12 | 98 |  | 3 |
|  |  | *Augochlorella aurata* | 7849 | 1 | 116 | 174 | 5701 | 15 | 96 | 339 | 359 | 6 | 1042 |
|  |  | *Augochlorella persimilis* | 21 |  |  | 8 |  |  |  |  | 13 |  |  |
|  |  | *Augochloropsis metallica* | 4 |  |  |  |  |  | 1 | 3 |  |  |  |
|  |  | *Halictus confusus* | 208 |  | 8 | 3 | 41 | 2 | 1 | 127 | 19 | 1 | 6 |
|  |  | *Halictus ligatus* | 463 |  | 5 | 7 | 130 | 2 |  | 256 | 60 |  | 3 |
|  |  | *Halictus parallelus* | 4 |  |  |  | 4 |  |  |  |  |  |  |
|  |  | *Halictus rubicundus* | 39 |  |  |  | 25 | 1 |  | 3 | 4 | 1 | 5 |
|  |  | *Lasioglossum abanci* | 8 |  |  |  | 1 |  |  |  | 6 |  | 1 |
|  |  | *Lasioglossum acuminatum* | 158 |  | 21 |  | 77 | 9 |  | 27 | 19 | 3 | 2 |
|  |  | *Lasioglossum admirandum* | 110 |  | 7 | 12 | 60 |  | 1 | 27 | 3 |  |  |
|  |  | *Lasioglossum albipenne* | 5 |  | 1 | 3 | 1 |  |  |  |  |  |  |
|  |  | *Lasioglossum anomalum* | 10 |  |  |  | 1 |  |  | 9 |  |  |  |
|  |  | *Lasioglossum apocyni* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Lasioglossum arantium* | 40 |  |  | 4 |  |  | 36 |  |  |  |  |
|  |  | *Lasioglossum ascheri* | 1 |  |  |  |  |  |  | 1 |  |  |  |
|  |  | *Lasioglossum birkmanni* | 4 |  |  |  |  |  |  | 1 | 3 |  |  |
|  |  | *Lasioglossum bruneri* | 112 | 2 |  | 7 | 23 | 1 | 9 | 21 | 45 | 4 |  |
|  |  | *Lasioglossum callidum* | 3 |  |  |  |  |  |  |  | 2 |  | 1 |
|  |  | *Lasioglossum cattellae* | 3 |  |  | 1 |  |  |  |  | 2 |  |  |
|  |  | *Lasioglossum cinctipes* | 3 |  |  |  |  |  |  | 2 |  |  | 1 |
|  |  | *Lasioglossum coeruleum* | 7 |  |  |  |  |  |  | 1 | 5 |  | 1 |
|  |  | *Lasioglossum coreopsis* | 6 |  |  | 6 |  |  |  |  |  |  |  |
|  |  | *Lasioglossum coriaceum* | 135 |  | 1 |  | 58 | 1 |  | 7 | 42 |  | 26 |
|  |  | *Lasioglossum cressonii* | 130 |  | 1 | 5 | 18 | 5 | 1 | 59 | 28 | 2 | 11 |
|  |  | *Lasioglossum ellisiae* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Lasioglossum ephialtum* | 49 | 3 | 1 |  |  | 1 |  | 37 | 6 |  | 1 |
|  |  | *Lasioglossum fattigi* | 4 |  |  |  |  | 4 |  |  |  |  |  |
|  |  | *Lasioglossum floridanum* | 123 |  |  | 122 |  | 1 |  |  |  |  |  |
|  |  | *Lasioglossum foxii* | 12 |  |  |  |  |  |  | 7 | 5 |  |  |
|  |  | *Lasioglossum fuscipenne* | 7 |  |  |  | 5 |  |  | 1 | 1 |  |  |
|  |  | *Lasioglossum georgeickworti* | 9 |  |  | 1 | 8 |  |  |  |  |  |  |
|  |  | *Lasioglossum gotham* | 3 |  |  |  |  |  |  |  | 2 |  | 1 |
|  |  | *Lasioglossum hitchensi* | 63 |  |  | 36 | 2 |  | 1 | 5 | 19 |  |  |
|  |  | *Lasioglossum imitatum* | 10 |  |  |  |  |  |  | 4 | 4 |  | 2 |
|  |  | *Lasioglossum inconditum* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Lasioglossum katherineae* | 46 |  | 35 |  |  | 6 |  | 1 | 4 |  |  |
|  |  | *Lasioglossum laevissimum* | 3 |  |  |  |  |  |  | 3 |  |  |  |
|  |  | *Lasioglossum leucocomus* | 794 | 1 | 130 | 3 | 411 | 13 |  | 140 | 67 |  | 29 |
|  |  | *Lasioglossum leucozonium* | 87 |  | 31 |  | 36 | 1 |  | 2 | 4 | 1 | 12 |
|  |  | *Lasioglossum lineatulum* | 12 |  |  |  | 1 |  |  | 8 | 2 |  | 1 |
|  |  | *Lasioglossum lustrans* | 2 |  |  | 2 |  |  |  |  |  |  |  |
|  |  | *Lasioglossum macoupinense* | 1 |  |  |  |  |  |  |  |  |  | 1 |
|  |  | *Lasioglossum marinum* | 8 |  |  |  | 8 |  |  |  |  |  |  |
|  |  | *Lasioglossum michiganense* | 1 |  |  |  |  |  |  | 1 |  |  |  |
|  |  | *Lasioglossum nelumbonis* | 22 |  |  | 1 |  |  | 2 |  | 19 |  |  |
|  |  | *Lasioglossum nigroviride* | 1 |  |  |  |  |  |  |  | 1 |  |  |
|  |  | *Lasioglossum nymphale* | 26 |  |  |  |  |  | 26 |  |  |  |  |
|  |  | *Lasioglossum oblongum* | 42 | 2 |  | 2 | 4 | 6 | 8 |  | 16 |  | 4 |
|  |  | *Lasioglossum oceanicum* | 324 |  | 3 |  | 319 |  |  |  | 1 |  | 1 |
|  |  | *Lasioglossum oenotherae* | 1 |  |  |  | 1 |  |  |  |  |  |  |
|  |  | *Lasioglossum paradmirandum* | 5 |  |  |  |  |  |  |  | 5 |  |  |
|  |  | *Lasioglossum paradmirandum?* | 1 |  |  |  | 1 |  |  |  |  |  |  |
|  |  | *Lasioglossum pectorale* | 312 | 2 |  | 1 | 228 | 2 |  | 48 | 11 | 2 | 18 |
|  |  | *Lasioglossum pilosum* | 272 |  | 5 | 13 | 4 | 1 | 1 | 140 | 105 |  | 3 |
|  |  | *Lasioglossum planatum* | 4 | 1 |  |  | 1 | 1 |  | 1 |  |  |  |
|  |  | *Lasioglossum pruinosum* | 110 |  | 11 |  | 98 | 1 |  |  |  |  |  |
|  |  | *Lasioglossum quebecense* | 15 |  |  |  |  | 2 |  |  | 10 | 3 |  |
|  |  | *Lasioglossum rozeni* | 4 |  |  | 1 |  |  |  |  | 3 |  |  |
|  |  | *Lasioglossum smilacinae* | 10 |  | 2 |  | 2 | 3 | 2 |  | 1 |  |  |
|  |  | *Lasioglossum sopinci* | 39 |  |  | 1 |  |  | 38 |  |  |  |  |
|  |  | *Lasioglossum subviridatum* | 50 |  |  | 1 | 5 | 17 | 3 | 1 | 22 |  | 1 |
|  |  | *Lasioglossum taylorae* | 19 |  | 3 |  |  | 14 |  | 1 | 1 |  |  |
|  |  | *Lasioglossum tegulare* | 235 | 3 | 2 | 29 | 105 | 2 | 1 | 33 | 59 |  | 1 |
|  |  | *Lasioglossum timothyi* | 60 |  | 3 |  | 1 | 9 |  | 47 |  |  |  |
|  |  | *Lasioglossum trigeminum* | 66 | 1 |  | 15 |  | 1 | 1 |  | 48 |  |  |
|  |  | *Lasioglossum truncatum* | 25 |  |  |  |  |  |  | 2 | 23 |  |  |
|  |  | *Lasioglossum versans* | 6 |  |  | 1 |  |  |  | 3 | 2 |  |  |
|  |  | *Lasioglossum versatum* | 215 | 1 | 2 | 45 | 13 | 1 | 1 | 63 | 56 |  | 33 |
|  |  | *Lasioglossum vierecki* | 460 |  |  | 42 | 3 |  |  | 385 |  |  | 30 |
|  |  | *Lasioglossum viridatum* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Lasioglossum weemsi* | 3 |  |  | 2 |  |  |  |  | 1 |  |  |
|  |  | *Lasioglossum wheeleri* | 2 |  |  |  |  |  |  |  | 2 |  |  |
|  |  | *Lasioglossum zonulum* | 74 |  |  | 1 | 2 |  |  | 2 | 69 |  |  |
|  |  | *Sphecodes aroniae* | 3 |  | 1 |  | 1 |  |  |  |  |  | 1 |
|  |  | *Sphecodes banksii* | 14 |  |  |  |  |  |  | 14 |  |  |  |
|  |  | *Sphecodes brachycephalus* | 1 | 1 |  |  |  |  |  |  |  |  |  |
|  |  | *Sphecodes carolinus* | 1 |  |  |  | 1 |  |  |  |  |  |  |
|  |  | *Sphecodes confertus* | 2 |  |  |  |  |  |  |  | 1 |  | 1 |
|  |  | *Sphecodes coronus* | 1 |  |  |  |  |  |  |  |  |  | 1 |
|  |  | *Sphecodes davisii* | 47 |  |  |  |  |  |  | 28 | 7 |  | 12 |
|  |  | *Sphecodes fattigi* | 6 |  |  |  |  |  |  | 1 | 5 |  |  |
|  |  | *Sphecodes galerus* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Sphecodes heraclei* | 2 |  |  |  |  |  |  | 2 |  |  |  |
|  |  | *Sphecodes illinoensis* | 1 |  |  |  |  |  |  | 1 |  |  |  |
|  |  | *Sphecodes johnsonii* | 6 |  |  |  |  |  |  |  | 1 |  | 5 |
|  |  | *Sphecodes mandibularis* | 39 |  |  | 1 | 13 |  | 2 | 22 | 1 |  |  |
|  |  | *Sphecodes pimpinellae* | 6 |  |  |  | 5 |  |  |  | 1 |  |  |
|  |  | *Sphecodes ranunculi* | 1 |  |  |  |  |  |  | 1 |  |  |  |
|  |  | *Sphecodes townesi* | 1 |  |  |  |  |  |  |  |  |  | 1 |
| Megachilidae | Megachilinae | *Anthidiellum notatum* | 4 | 1 |  | 1 |  |  |  | 1 | 1 |  |  |
|  |  | *Anthidium manicatum* | 2 |  | 1 | 1 |  |  |  |  |  |  |  |
|  |  | *Anthidium oblongatum* | 2 |  |  |  |  | 1 |  | 1 |  |  |  |
|  |  | *Coelioxys alternata* | 1 |  |  |  |  |  |  | 1 |  |  |  |
|  |  | *Coelioxys immaculata* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Coelioxys octodentatus* | 1 |  |  |  | 1 |  |  |  |  |  |  |
|  |  | *Coelioxys rufitarsis* | 4 |  | 1 |  | 1 |  |  |  |  |  | 2 |
|  |  | *Coelioxys sayi* | 8 |  |  | 2 |  |  |  |  | 1 |  | 5 |
|  |  | *Heriades carinata* | 5 |  |  |  |  |  | 1 | 1 | 2 |  | 1 |
|  |  | *Hoplitis pilosifrons* | 105 |  | 8 | 9 | 18 |  |  | 23 | 9 |  | 38 |
|  |  | *Hoplitis producta* | 48 |  |  | 4 |  |  |  | 25 | 9 |  | 10 |
|  |  | *Hoplitis simplex* | 3 |  |  |  |  |  |  |  | 3 |  |  |
|  |  | *Hoplitis spoliata* | 8 |  | 1 | 1 |  |  |  | 2 | 2 | 1 | 1 |
|  |  | *Hoplitis truncata* | 21 |  |  | 2 | 2 | 2 |  | 15 |  |  |  |
|  |  | *Megachile addenda* | 38 |  |  | 3 | 35 |  |  |  |  |  |  |
|  |  | *Megachile brevis* | 85 |  | 7 | 1 | 73 |  |  | 2 | 1 |  | 1 |
|  |  | *Megachile campanulae* | 10 | 1 |  |  |  |  |  | 1 | 8 |  |  |
|  |  | *Megachile exilis* | 8 |  |  | 2 |  |  |  |  | 1 |  | 5 |
|  |  | *Megachile frugalis* | 3 |  |  |  |  |  |  |  | 3 |  |  |
|  |  | *Megachile gemula* | 1 |  |  |  |  |  |  |  | 1 |  |  |
|  |  | *Megachile inermis* | 2 |  |  |  |  |  |  | 2 |  |  |  |
|  |  | *Megachile inimica* | 3 |  |  |  |  |  |  | 3 |  |  |  |
|  |  | *Megachile latimanus* | 29 |  | 13 |  | 9 |  |  | 1 | 1 |  | 5 |
|  |  | *Megachile mendica* | 51 |  |  | 12 | 17 |  |  | 5 | 12 |  | 5 |
|  |  | *Megachile montivaga* | 5 |  |  |  |  |  |  | 5 |  |  |  |
|  |  | *Megachile petulans* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Megachile pugnata* | 6 |  |  | 2 |  |  |  | 3 | 1 |  |  |
|  |  | *Megachile relativa* | 10 |  |  |  |  |  |  | 8 | 2 |  |  |
|  |  | *Megachile rotundata* | 1 |  |  |  |  |  |  | 1 |  |  |  |
|  |  | *Megachile sculpturalis* | 11 |  |  |  |  |  |  |  |  |  | 11 |
|  |  | *Megachile texana* | 10 |  |  | 7 |  |  |  | 2 | 1 |  |  |
|  |  | *Megachile xylocopoides* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Osmia albiventris* | 7 |  |  | 2 |  | 2 |  | 1 | 1 |  | 1 |
|  |  | *Osmia atriventris* | 36 | 1 | 5 | 1 | 10 | 1 |  | 9 | 2 |  | 7 |
|  |  | *Osmia bucephala* | 10 |  |  | 2 |  | 2 |  | 1 | 2 |  | 3 |
|  |  | *Osmia collinsiae* | 10 |  | 6 |  |  | 3 |  |  | 1 |  |  |
|  |  | *Osmia conjuncta* | 4 |  |  | 4 |  |  |  |  |  |  |  |
|  |  | *Osmia cornifrons* | 7 |  |  |  |  |  |  | 1 |  |  | 6 |
|  |  | *Osmia distincta* | 3 |  |  | 1 |  |  |  |  |  |  | 2 |
|  |  | *Osmia georgica* | 30 |  |  |  | 3 | 1 |  |  | 25 |  | 1 |
|  |  | *Osmia inspergens* | 2 |  |  |  |  | 1 |  |  | 1 |  |  |
|  |  | *Osmia lignaria* | 4 |  |  | 2 |  |  |  |  | 2 |  |  |
|  |  | *Osmia pumila* | 105 | 1 |  | 5 | 7 | 3 | 4 | 7 | 27 | 4 | 47 |
|  |  | *Osmia sandhouseae* | 4 |  |  | 2 |  | 2 |  |  |  |  |  |
|  |  | *Osmia simillima* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Osmia subarctica* | 1 |  |  |  |  |  |  |  |  |  | 1 |
|  |  | *Osmia subfasciata* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Osmia texana* | 1 |  |  | 1 |  |  |  |  |  |  |  |
|  |  | *Osmia virga* | 36 |  | 3 |  |  | 9 | 4 | 10 | 10 |  |  |
|  |  | *Paranthidium jugatorium* | 1 |  |  |  |  |  |  |  | 1 |  |  |
|  |  | *Stelis labiata* | 1 | 1 |  |  |  |  |  |  |  |  |  |
|  |  | *Stelis lateralis* | 13 |  |  |  | 1 |  |  | 2 |  |  | 10 |
|  |  | *Stelis louisae* | 3 |  |  |  |  |  |  |  | 3 |  |  |
|  |  | *Stelis subemarginata* | 1 |  |  |  |  | 1 |  |  |  |  |  |
| Melittidae | Melittinae | *Macropis ciliata* | 3 |  |  |  |  |  |  | 2 | 1 |  |  |
|  |  | *Macropis nuda* | 5 |  | 5 |  |  |  |  |  |  |  |  |

# Appendix B: Taxonomic Notes

Apidae Ceratina "Ceratina mikmaqi": This is a recent taxonomic split from dupla and calcarata

Lasioglossum:
L. arantium: newly described in Gibss 2011
L. ellisiae: recently separated from L. tegulare in Gibbs 2009
L. ephialtum: newly described in Gibbs 2010
L. floridanum: recently separated from L. pilosum Gibbs 2010
L. georgeickworti: newly described species in Gibbs 2011
L. gotham: newly described species in Gibbs 2011
L. hitchensi: formerly Lasioglossum mitchelli
L. katherineae: newly described species in Gibbs 2011
L. leucocomus: recently separated from L. pilosum Gibss 2010 (aka leucocomum in National Bee Tool)
L. oceanicum: formerly L. Nymphaearum
L. planatum: recently separated from L. Oblongum Gibbs 2010
L. rozeni: newly described species in Gibbs 2011
L. smilacinae: previously known as L. zophops
L. taylorae: newly described species in Gibbs 2010
L. timothyi: newly described species in Gibbs 2010
L. trigeminum: newly described species in Gibbs 2011