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ORIGINAL PAPER

Floral Visitation and Pollen Collection by Native Bees in Temperate Deciduous Forests with Diverse Understory Communities

Lucia R. Weinman[1,2,3] · **Katherine J. Turo**[3] · **Trent Ress**[3] · **Rachael Winfree**[3]

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Abstract

The native bees associated with deciduous forest are likely the pre-colonial dominant bee fauna of the eastern United States, yet we lack the data on their resource use needed to guide management. We characterized bees' floral resource use in mature deciduous forests managed by the National Park Service at sites spanning ~ 550 km of latitude in Indiana and Michigan. We collected floral visitation records for 4194 bee specimens representing 103 species, and data on bees' pollen collection for 665 specimens. Our findings highlight differences among dominant bee genera in their floral resource use, especially pollen, and confirm the importance of canopy tree species and shrubs for bees in deciduous forests, even in those with diverse understory floral assemblages. As the largest, most spatially extensive source of data on bees' use of floral resources within mature deciduous forests in North America, these records provide a useful reference point for forest bee conservation.

Keywords Temperate broadleaf forest · Wild bees · Floral resources · Pollen analysis · Canopy ecology · Understory plant diversity

Study Implications Forests are considered important bee habitat, but little data exist on bees' use of forest plant species, including deciduous trees and shrubs. Across three National Parks in the upper Midwest, we found that bees in mature deciduous forests predominantly collected pollen from native spring understory herbs, willows, and maple trees, but bee genera varied greatly in their pollen use. This diversity of foraging behavior suggests that forestry practices that encourage flowering plant diversity are also likely to enhance forest bee communities. Likewise, because we found that canopy and shrub flowers were common pollen resources, even in a mature, ecologically intact deciduous forest, our findings suggest that we should explicitly consider flowering trees and shrubs in future assessments of forests' value for pollinators.

Extended author information available on the last page of the article

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Introduction

Forests are increasingly recognized as critical habitat for native bee species globally (Ulyshen et al. 2023), yet bee communities in forests have been relatively understudied. In the United States and Canada, for example, entomological research in deciduous and coniferous forests has focused on insect pests and detritivores (Ayres and Lombardero 2000; Ramsfield et al. 2016), while bee ecology and conservation research has predominantly occurred in agricultural and other open, meadow-type natural and anthropogenic habitats (Winfree 2010; Ulyshen et al. 2023). Thus, as the consensus grows that forests provide important habitat for native bees, and land managers are increasingly called upon to consider how their forest management affects bee species, many aspects of forest bee ecology remain underexplored (Ulyshen et al. 2023).

One aspect of bee ecology that is especially important but is still understudied in most forest contexts, is bees' use of floral resources (Menz et al. 2011; Winfree 2010). Bees obtain all of their food from flowers in the form of pollen and nectar, and bee populations are generally thought to be limited by the availability of floral resources (Roulston and Goodell 2011; Goulson et al. 2015). Plants can vary in their attractiveness to bees, though, and bee taxa often differ in their floral preferences, the flexibility of their diet, and the richness of resources they require (Cane and Sipes 2006; Minckley and Roulston 2006; reviewed in Danforth et al. 2019). Additionally, bees' floral use in forests likely varies with forest context, as forests offer different resources to bees depending on their stand composition, understory plant communities, underlying disturbance regimes, invasion history, and phenology of flowering resources. Despite this, we lack basic data on bees' floral use for even broad categories of coniferous or deciduous forests across most biogeographic regions (Ulyshen et al. 2023). Developing a nuanced understanding of how bee communities exploit floral resources in a range of forest types will be foundational to developing effective management strategies for bees in forests.

In the eastern United States, broadleaf deciduous forest habitat hosts a phenologically and taxonomically distinct native bee fauna that is not well supported by current bee conservation practices, which focus on open meadow-type habitats (Wood et al. 2018; Harrison et al. 2018). Bee abundance in mature deciduous forests peaks in the springtime (Harrison et al. 2018), coinciding with the bloom of woody shrubs, canopy trees, and the spring ephemeral wildflowers, which bees have long been known to pollinate (Macior 1978; Schemske et al. 1978; Motten 1986). Bees in this forest type tend to belong to a different subset of bee genera than those bees that are active in the summertime and are most prevalent in more open natural and anthropogenic habitats (Harrison et al. 2018). In addition, many bee species have been identified as either forest specialists on deciduous forest or as habitat generalists that are equally abundant in both deciduous forests and urban or agricultural habitats (Smith et al. 2021). A few recent studies have characterized bees' use of floral resources in deciduous forests by quantifying floral visitation or pollen collection by spring-flying bees in the Northeastern and upper-Midwestern USA (e.g., Russo and Danforth 2017; Wood et al. 2018; Wood

and Roberts 2018; Smith et al. 2019; Urban-Mead et al. 2021, 2023; Winfree et al. 2014). While these studies do provide information about resource use for many bee species, they have predominantly occurred along deciduous forest edges, or in agricultural contexts and other non-forest habitats. Those that have sampled bees within interior deciduous forest habitat have done so in forests whose understories are degraded by deer grazing and invasive plant species (e.g., Smith et al. 2019). Therefore, while the recent efforts cited above provide valuable information about how bees are currently foraging in deciduous forests with degraded understories and intermixed non-forest habitat, we still lack knowledge of how bees forage in mature deciduous forests when they have access to the abundance and diversity of native flowering plants with which they likely coevolved, including the understory herbs that are now missing from many forests (Kelly 2019).

Widespread degradation of eastern deciduous forest understories poses a challenge not only to understanding how native bees forage on native understory plants, but also to bees' relative use of understory versus canopy resources. A number of lines of evidence suggest that canopy tree species and other woody plants are important resources for forest bees. Trees such as maples and willows have long been known to provide important pollen resources early in the season when few other plants are flowering (Batra 1980, 1990). Several recent surveys of eastern deciduous forest canopies have found high abundance and diversity of bees foraging on canopy trees, including wind-pollinated species such as oaks and beech (Urban-Mead et al. 2021; Ulyshen et al. 2020; Ulyshen et al. 2010), and forest tree composition appears to affect bee community composition (Traylor et al. 2024; Ulyshen et al. 2024). The handful of studies that characterize spring-flying bees' collection of pollen show that pollens from spring-flowering trees and shrubs are important to many bee species in forest-associated bee genera (Russo and Danforth 2017; Wood et al. 2018; Wood and Roberts 2018; Smith et al. 2019; Urban-Mead et al. 2023). Yet this apparent importance of canopy trees and other woody plants could be a legacy of the recent anthropogenic factors that have degraded forest understories. Eastern deciduous forests now predominantly host understories with much lower floral resource abundance and diversity than they did historically due to the slow recolonization of native herbs in second growth forests following agricultural land use, the effects of widespread deer browse and species invasions, and other factors (Rooney et al. 2004; Rooney 2009; Aronson and Handel 2011; Kain et al. 2011; Kelly 2019; Flinn and Vellend 2005). As a result, it remains unclear to what extent bees generally prefer canopy resources and other woody plants, or simply choose to collect pollen from canopy trees and other woody plants due to a scarcity of high-quality herbaceous understory resources (Ulyshen et al. 2023).

Pollen analysis, or taxonomic identification of the grains of pollen that female bees intentionally collect to provision their larvae, is a particularly powerful tool for identifying the plants bees depend on, for several reasons. First, pollen is an important resource for bees, as it provides proteins and lipids essential for developing bee larvae (Michener 2000). A number of components of female bee fitness – the number of offspring produced, offspring body size, and offspring sex ratio – are positively related to the amount of pollen females are able to collect (Bosch 2008; Kim 1999). Bee species are thought to be more specialized in terms of the plants from

which they collect pollen, as compared with those they nectar on, and bee species are also thought to differ more from each other in their collection of pollen than nectar (Danforth et al. 2019). Second, pollen analysis is an excellent tool for evaluating bees' relative use of canopy versus understory resources, because it allows for quantification of bees' collection of canopy pollens without making direct observations of bees' foraging activities in the forest canopy, which is typically out of reach for field workers (Smith et al. 2019; Urban-Mead et al. 2023). Finally, comparing data on bees pollen collection with visitation records can provide insight into the effectiveness of visitation data for characterizing bees' diets, as well as which plant species are visited primarily as sources of nectar rather than pollen (Alarcón 2010; Tur et al. 2014; Librán-Embid et al. 2024).

Here, we characterize bees' use of floral resources within mature, second-growth deciduous forests which span ~ 550 km of latitude in of northern Indiana and Michigan. We focused on forests managed by the National Park Service that have not been harvested in approximately 100 years and that host diverse spring ephemeral understory communities (Paulson et al. 2016; Haswell and Alanen 1994). These forests are actively managed by the National Park Service to control invasive understory plant species and deer populations. All feature large areas of understory that host abundant and diverse herbaceous understory plants, providing an opportunity to examine how bees in mature eastern deciduous forests provision larvae when they have access to a high abundance of native understory resources. To obtain data on bees' floral associations, we collected foraging bees, and used light microscopy to identify and count the pollen grains found in foragers' scopa (pollen-collecting structures). We use these data to characterize the floral resources bees use in mature eastern deciduous forests, including bees' relative pollen collection from trees and shrubs, as compared with herbaceous flowers, and foraging differences among bee genera. We also assess how bees' floral associations differ when characterized using floral visitation versus scopal pollen data.

Methods

Data Collection

Study sites – We collected bee specimens in April, May and June of 2018 and 2019, at twelve study sites in three National Parks of the Upper Midwest. We sampled during the spring season because this is the time of year when bee abundance peaks in mature eastern deciduous forest habitats (Harrison et al. 2018). The three parks are separated by ~ 190–560 km of latitudinal distance (Fig. 1). The latitudinal distance between pairs of adjacent parks separates the phenology of each park by about 2 weeks (D. Robertson-Thompson, pers. comm.; First author, pers. obs.). We took advantage of this phenological lag time to match our sampling at each park with the bloom time of dominant understory herbs and maples (Figure S1). One site was located within the Moraine Nature Preserve in Indiana; the remaining eleven sites were located within three National Parks in Indiana and Michigan: Indiana

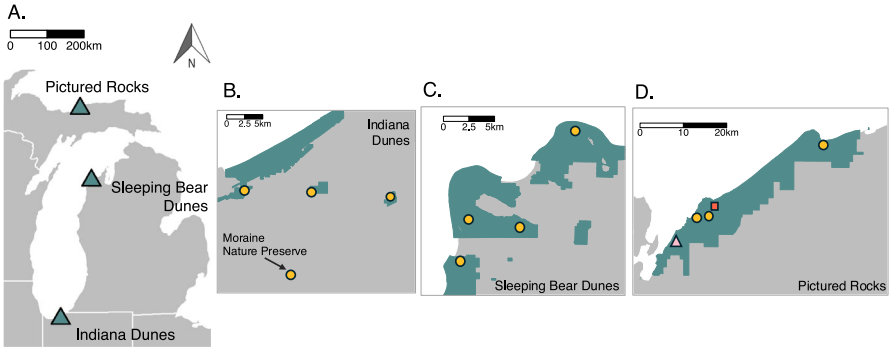

Fig. 1 **A**) Map of study region, with teal triangles indicating locations of National Parks at which we sampled. **B**-**D**) Sampling locations at Indiana Dunes National Park and Moraine Nature Preserve (panel B), Sleeping Bear Dunes National Lakeshore (panel C), and Pictured Rocks National Lakeshore (panel D). Park boundaries are in teal. Yellow circles indicate sites that were sampled in both years of the study, while the red square indicates the site we sampled only in 2018, and the pink triangle indicates the site sampled only in 2019

Dunes National Park, Sleeping Bear Dunes National Lakeshore, and Pictured Rocks National Lakeshore (Fig. 1).

Sites were located within mature second-growth deciduous forests that vary in their land use history, and in the level of deer browse and invasive species pressure they experience. These forests are actively managed by the National Park Service to control deer pressure and invasive plant species, and to maintain overall forest health, though the specifics of management vary among forest stands and among parks (Methods S1). Consequently, at each park there are large areas of diverse native understory plant communities, including insect-pollinated spring ephemeral species and other spring herbs that are sensitive to deer and invasive species pressure and thus are now uncommon throughout much of the Northeastern and upper-Midwestern United States (Kelly 2019; Rooney et al. 2004; K. D. Hop et al. 2009; K. Hop et al. 2010; K. D. Hop et al. 2011). Thus, our data provide insight into how bees forage in the areas of mature, maple-dominated deciduous forest where diverse native understory resources are available to them. In Indiana, the forests we sampled were North Central Interior Beech-Maple and Maple-Basswood forests; in Michigan, they were Laurentian-Acadian Northern Hardwood forests with maple-beech and maple-birch overstories (K. Hop et al. 2010; K. D. Hop et al. 2009, 2011). Other deciduous forest types were represented in the landscape at each park, but we chose sites within these forest types because they were the most similar to each other in plant composition and understory phenology across the three National Parks (K. Hop et al. 2010; K. D. Hop et al. 2009, 2011). Sparse forest shrub layers were characterized by the early-spring flowering shrub spicebush (*Lindera benzoin*), and occasionally included species of serviceberry (*Amelanchier*), elderberry (*Sambucus*), native honeysuckle (*Lonicera*) and gooseberry (*Ribes*). Forest understories were dominated by insect-pollinated spring herbs, especially spring beauty (*Claytonia*), trout lily (*Erythronium*), violets (*Viola*), Dutchman's britches (*Dicentra*) and bittercress (*Cardamine*).

In order to collect as much data as possible on the most bee species, and to learn how bees forage in mature deciduous forests when they have access to abundant and diverse understory resources, we selected sites in areas of each forest at the high end of understory floral abundance and diversity for that forest (First author, pers. obs). To do this, we identified potential sites in each forest that were accessible from trails and roadsides and hosted flowering understory plant communities likely to have high bee activity. We then chose the four sites with the highest abundance and diversity of resources that could also be spaced at least 1.5 km apart, beyond the foraging range of most bee species, in order to ensure independence of data collected at different sites. When greater than four sites were available to us within a park that met the above criteria, we chose the sites that appeared to have the highest floral abundance and diversity. When extra sites were similar in floral abundance and diversity, we chose among them at random using the *sample* function in R. Sites were approximately one hectare in area, and located a median of 455 m from forest edge (range: 92–2404 m), with a median of 71% forest cover at a 1 km radius (range: 0.52–0.97) (Dewitz 2021). Within parks, sites were separated by a median distance of 11 km (range: 1.7–39 km).

Bee specimen collection — To collect data on bee communities and bees' plant associations, we used insect nets to collect bees as they foraged on flowers in the forest understory. We sampled each site at each park 2–4 times within a 2–3 week period. We only sampled on clear, bright days when the temperature was at least 13° C. To sample a site, two to three field workers began net collecting bees in the morning as soon as the temperature reached 13° C or bee activity was observed, and continued netting until bee activity ceased. For the 11 sites that were sampled in both years of the study, this resulted in a mean of 20 person-hours of sampling per site (range 14–34 person-hours); sampling effort varied among sites due to weather and other logistical constraints (Table S1). We evaluated sample completeness by measuring sample coverage, which is an estimate of the proportion of all individuals in a community that belong to species captured by a sample of that community (Chao and Jost 2012; Roswell et al. 2021). We measured sample coverage using the iNEXT package in R (Hsieh et al. 2016).

At each site, we used insect nets to opportunistically collect bees wherever we encountered them within the area of the study site. To ensure that samples were not biased to narrow areas of each site, we divided the site into three smaller sampling areas, and ensured that field workers systematically rotated among these smaller sampling areas over the course of the day. Within each smaller sampling area, we walked in a zigzag fashion throughout the area, pausing when we encountered bee activity to collect specimens, and moving on when activity had ceased. We transferred each bee specimen individually into a clean vial to prevent pollen contamination between specimens, and recorded the plant species the specimen was foraging on at the time we collected it. To minimize bees' grooming activities and other movements which could disturb the distribution of pollen on their bodies and pollen-collecting structures, we then placed specimens on ice in a portable cooler while still in the field. To kill bee specimens, we froze them in a − 20° C freezer overnight. Bee specimens were later identified to species by Julia Criscione at Rutgers University and by Joel Gardner at the University of Manitoba. Bee specimens

in the genus *Nomada* were identified by Sam Droege at the USGS Eastern Ecological Science Center. A list of references used in support of bee identification can be found in the supplemental material (Methods S2). All bee specimens are curated in the last author's lab collection at Rutgers University.

One highly abundant pollen-specialist species, *Andrena erigeniae*, comprised 12% of all bee specimens we collected. Because *A. erigeniae* is a narrow pollen specialist on two species in the genus *Claytonia* (Davis Jr. and LaBerge 1975), assessing *A. erigeniae* foraging is unlikely to tell us anything about its pollen collection that we do not already know. We therefore omit specimens of *A. erigeniae* from analysis of floral visitation data and identification of scopal loads, though visitation records of this species are reported in Table S2.

Pollen Methods

In addition to data on bees' floral visitation, we also collected data on bees' collection of pollen by identifying the grains of pollen that female specimens had collected into their scopae and corbiculae. Because identifying pollen is time-consuming, it was not practical to conduct pollen analysis on the scale of the entire dataset. We therefore limited pollen analysis to a subset of specimens in a number of ways. To ensure that we only included data from bees that were actively foraging for pollen and minimize inclusion of pollen grains that have incidentally attached themselves to scopal hairs, we limited pollen identification to female bee specimens that had stored a minimum of 50 grains of pollen in their scopae or corbiculae. We also deliberately omitted specimens of 1) the kleptoparasitic genus *Nomada*, as females of this taxon lay their eggs in the nests of other bee species and do not collect pollen to provision larvae themselves, and 2) the aforementioned pollen-specialist species *Andrena erigeniae*. Finally, from the remaining female specimens, we selected a subset of 677 specimens representing 47 bee species for which to identify pollen in scopal and corbiculate pollen loads. There are four bee species that are especially abundant in this subset relative to their abundance in the larger visitation dataset, comprising 61% of specimens; these were *Andrena erythronii*, *Andrena rugosa*, *Lasioglossum quebecense*, and *Bombus bimaculatus*. These species are especially abundant in the pollen data for two reasons. One, bee species differed in the proportion of specimens that were female, and that were carrying pollen loads, such that some bee species are naturally underrepresented in the pollen data. Two, we chose to focus pollen analysis on a few, dominant species that were widespread across study sites, to provide in-depth information on their pollen use across the region, and most other bee species were present from only one or two sites. Because the focus on these four bee species biases pollen data towards the pollen use of these species, we conducted two sets of analyses of the pollen data – one using all specimens, and one excluding these species.

To obtain the scopal pollen from each bee specimen, we removed the hind legs of each specimen and placed them both into a microcentrifuge tube containing 95% ethanol. For specimens in the Megachilidae, which have abdominal scopae, we scraped bees' abdomens with forceps to remove scopal pollen and deposited the pollen into a microcentrifuge tube containing 95% ethanol. Microcentrifuge tubes were

then placed in an ultrasonic bath for 15 min to remove any pollen grains still sticking to scopae or corbiculae. To stain pollen samples and mount them onto microscope slides for identification, we first spun samples in a microcentrifuge at 1000 rpm for 2 min. For each sample, we then melted two cubes of fuchsin gel on a glass slide and pipetted two 5ul aliquots of highly concentrated pollen solution directly into the molten gel.

To curate a pollen reference library for use in pollen identification, we collected pollen samples from as many plant taxa as possible and mounted them on to glass slides with molten fuchsin gel. Reference samples were obtained in several ways to maximize pollen library coverage. On each sample date, we obtained freshly dehisced anthers from all plant species with open flowers at each site, surveying a ~ 3 ha area around the center of each site for plants with open flowers. We also collected dehisced anthers from woody plants common in the landscape that were not present within or near sites, or whose flowers were inaccessible within our site area because they are in the canopy, such as tree species in the genera *Salix, Quercus, Betula*, and *Acer.* All plants from which we collected anthers were identified to the species level in the field except for those in the genus *Salix*. For tree and shrub species that we knew to be present in the landscape, but for which we were unable to locate accessible individuals in the field, we collected pollen samples from herbarium specimens housed in the Chrysler Herbarium at Rutgers University. In total, we collected pollen reference samples from 127 plant taxa. This includes the 48 plant species that we directly observed bees to visit as we collected them.

Pollen identification – We identified pollen in body and scopal pollen samples to the finest taxonomic resolution possible using light microscopy. To identify pollen grains, we compared the appearance of grains to the reference library of pollen samples at 400 × magnification. We were not able to distinguish some plant species by their pollen, and so in some cases we use genus, family or higher-level groupings (Table S3). Additionally, we used morphospecies identifications for types of pollen which were not in our pollen reference library and that we were not able to otherwise identify. One of these morphospecies was especially abundant in samples, comprising 9% of bees' overall pollen collection; we were able to identify the taxonomic identity of this morphospecies as belonging to the genus *Viola* using molecular methods (Methods S3, Table S4). The remaining pollen morphospecies that were not in our reference library comprised only 3.4% of pollen grains found in scopal samples. Hereafter, we refer to all unique types of pollen as "pollen morphogroups."

We estimated the precision of pollen identifications by re-identifying the grains in the scopal pollen samples of a random subset of 46 specimens and calculating the proportion of all grains for which identifications differed between the original identification and the re-identification. Our error rate calculated in this way was 3.3%.

To estimate the percent composition of each pollen morphogroup in scopal pollen samples, we identified a maximum of 100 grains of pollen per slide. To minimize the sampling bias potentially introduced by the spatial clumping of pollen on the slides, we systematically scanned the fuchsin-stained areas of the slide at regularly spaced intervals. We conducted scans until we had either counted 100 grains of pollen or had covered the entire area of the slide that contained fuchsin-stained pollen, whichever came first. We counted 100 grains of pollen for all slides having at least

100 grains (89% of pollen samples) and between 50 and 100 grains for the remaining 11% of slides which contained fewer than 100 grains, and for which we had scanned the entire area of the slide containing fuchsin. To minimize inclusion of pollen morphogroups that bees had picked up incidentally from the environment, or that were present only by contamination, we omit records of pollen morphogroups comprising 2% or less of each sample (Tur et al. 2014). Identifications and counts for all pollen samples were obtained by a single observer.

Analysis

Overall Floral Resource Use, and Differences Among Bee Genera

Observations of bees' visits to flowers can tell us, broadly, which plants bees forage on, whether it be for nectar, pollen, or both resources. To assess bees' relative use of floral resources using visitation data, we calculated the total percentage of visits comprised by each plant species across all 3706 bee specimens and for each bee species. We also calculated the percentage of visits comprised by each plant species for each bee genus represented by at least 100 specimens. These genera were *Andrena, Augochlora, Colletes, Bombus, Lasioglossum, Nomada,* and *Osmia.*

Pollen analysis can tell us which plants female bees forage on for pollen in order to provision their larvae. Four bee species are disproportionately represented in the pollen dataset, which biases pollen data towards the pollen use of these species. We therefore conducted two sets of analyses of the pollen data – one using all specimens (the "full pollen dataset"), and one excluding these species (the "reduced pollen dataset").

To assess the bee community's relative collection of pollen from different plants, we calculated the total percentage of all pollen grains comprised by each pollen morphospecies across all 665 bee specimens for which we conducted pollen analysis. In addition, we also calculated the relative pollen collection for each bee genus represented by at least 50 specimens, i.e., *Andrena*, *Bombus, Colletes*, and *Lasioglossum*.

To assess the statistical significance of differences among bee genera in pollen collection, we conducted permutational multivariate analysis of variance (PERMANOVA). We used individual specimens' pollen loads as replicates, and the Bray–Curtis dissimilarity index to measure dissimilarity in pollen load composition (Anderson 2001; Barwell et al. 2015). We measured dissimilarity and ran PERMANOVAs using the *adonis* function in the R package *vegan* (Oksanen et al. 2014; R Core Team 2022). Regardless of bee genus identity, the composition of bees' pollen loads was likely to differ across parks, due to differences in plant community composition across our study region. Such regional differences could be conflated with differences between genera, given that the relative abundance of genera differed across parks. To account for this, we used the "strata" argument in the *adonis* function to constrain permutations to observations within each park. In this context, PERMANOVA answers the question: "Given differences in bees' pollen collection between parks, is the composition of pollen loads collected by individuals of the same bee genus more similar, on average, than is the composition of pollen loads

collected by bee individuals generally*?"*. We conducted PERMANOVA on both the full pollen dataset and the reduced pollen dataset.

Collection of Pollen from Trees and Shrubs

We calculated the percentage of pollen from tree and shrub species collected by bee specimens overall and by each bee genus in the pollen analysis. We group trees and shrubs together for this analysis because we were unable to visually distinguish pollen from different plant species in the Rosaceae, and this plant family contains both tree and shrub species that bloom in the spring and provide resources to spring-flying bee species (Wood and Roberts 2018; Russo and Danforth 2017; Smith et al. 2019). To determine if bee genera differed in the proportion of tree/shrub versus spring herb pollen that they collected, we modelled the proportion of tree and shrub pollen in each scopal load as a function of bee genus using generalized linear models with a binomial error structure. We fit the model using the *glm* function, and assessed the significance of the overall model using a likelihood ratio test, which we carried out using the function *lrtest()* in the package *lmtest* in R (Zeileis and Hothorn 2002; R Core Team 2022). To determine post-hoc which bee genera differed from each other in their collection of tree and shrub pollen, we conducted a Tukey test using the function *glht()* in the package *multcomp* in R (Hothorn et al. 2008). We fit models and conducted post-hoc tests on both the full pollen dataset and the reduced pollen dataset.

Floral Visitation Versus Scopal Pollen Collection

For each well-represented bee genus in our pollen data (i.e., *Andrena, Bombus, Colletes,* and *Lasioglossum)*, we descriptively compared bees' floral associations as determined by our observation of bees' visits to flowers with those determined by our identification of bees' scopal pollen. For this comparison, we used the subset of specimen data for which we had both floral visitation records and pollen data. We grouped plant species that bees visited according to their corresponding pollen morphospecies in order to compare floral associations at the same resolution.

Results

We collected 4194 bee specimens of 103 bee species in 15 genera while they foraged on flowers (Table S2). Specimens were dominated by the forest-associated genera *Andrena*, *Colletes*, *Bombus*, *Lasioglossum*, *Augochlora*, *Osmia*, and *Nomada* (Harrison et al. 2018; Smith et al. 2021). At the scale of each park, sample coverage of bee species richness ranged from 98.4–99.3%. Likewise, for richness of plant species visited by bees, sample coverage ranged from 99.8–99.9%, and for richness of pollen morphospecies collected by bees, sample coverage ranged from 97.6–98.0% (Table S1).

For the pollen analysis, we identified pollen in the scopal loads of 665 bee specimens belonging to 47 bee species in nine genera (Fig. 2, Table S1). Results of

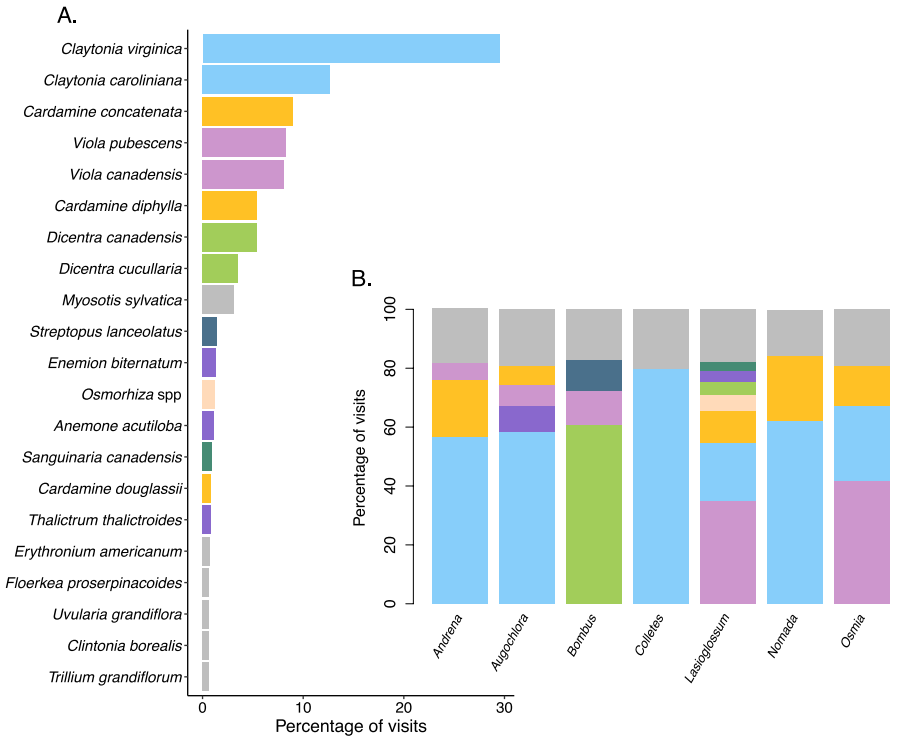

Fig. 2 **A**) The percentage of all bee specimens collected from each of the top 21 plant species representing 95% of visitation records. Plant species are color-coded by plant genus or family; note that *Enemion biternatum*, *Anemone acutiloba* and *Thalictrum thalictroides* are all members of the family Ranunculaceae (shown in dark purple) **B**) For each bee genus represented by at least 100 specimens, the percentage of specimens collected from each plant species. Plant species comprising the top 80% of visits for each bee genus are plotted in color and are grouped and color-coded according to plant genus or family; those comprising the bottom 20% are in gray

analyses of the full pollen dataset and the reduced pollen dataset were qualitatively similar, though dominant pollen moprhospecies collected by *Bombus* and *Lasioglossum* were different. We therefore report analysis of the full pollen dataset here, as well as the notable differences between the two datasets with respect to the resources used by *Bombus* and *Lasioglossum*, and report results of all other analyses of the reduced pollen dataset in the supplement (see Tables S6-S7 and Figures S2-S5).

Overall Floral Resource Use, and Differences Among Bee Genera

Bee specimens visited 48 plant species belonging to 28 plant families (Table S3). The distribution of bees' visits to plant species was highly skewed; the top eight most-highly visited plant species comprised 82% of bees' visits to plants, and the top 21 plant species comprised 95% of all visits (Fig. 2). Six plant species in the genera *Claytonia*, *Cardamine,* and *Viola* were highly visited by most bee genera, but

bee genera differed in which of these species they visited the most (Fig. 2). The genera *Andrena*, *Colletes*, *Augochlora* and *Nomada* primarily visited *Claytonia*, while *Lasioglossum* and *Osmia* primarily visited *Viola*. Bees in the genus *Bombus* showed the least overlap with other bee genera in the plants they visited; nearly all *Bombus* exclusively visited *Dicentra* species and *Streptopus lanceolatus*.

We observed pollen belonging to 47 pollen morphospecies in bees' scopal loads (Table S4). The top 20 of these morphospecies accounted for ~95% of bees' pollen collection (Fig. 3). Dominant bee genera differed in the plant taxa from which they collected pollen, and these differences were found to be statistically significant using PERMANOVA (pseudo-$R^2 = 0.16$, $F = 41.16$, $p = 0.001$). The bee genera *Andrena* and *Colletes* were similar to each other in their pollen collection, but both differed from *Bombus* and *Lasioglossum,* which also differed from each other (Fig. 3). Specimens of *Andrena* predominantly collected pollen from spring ephemerals in the Brassicaceae such as *Cardamine concatenata* and *Cardamine diphylla*, maple species, willow species, and spring ephemeral species in the genera *Claytonia* and *Erythronium.* Similar to *Andrena* spp., specimens of *Colletes inaequalis* collected pollen primarily from species in the Brassicaceae,

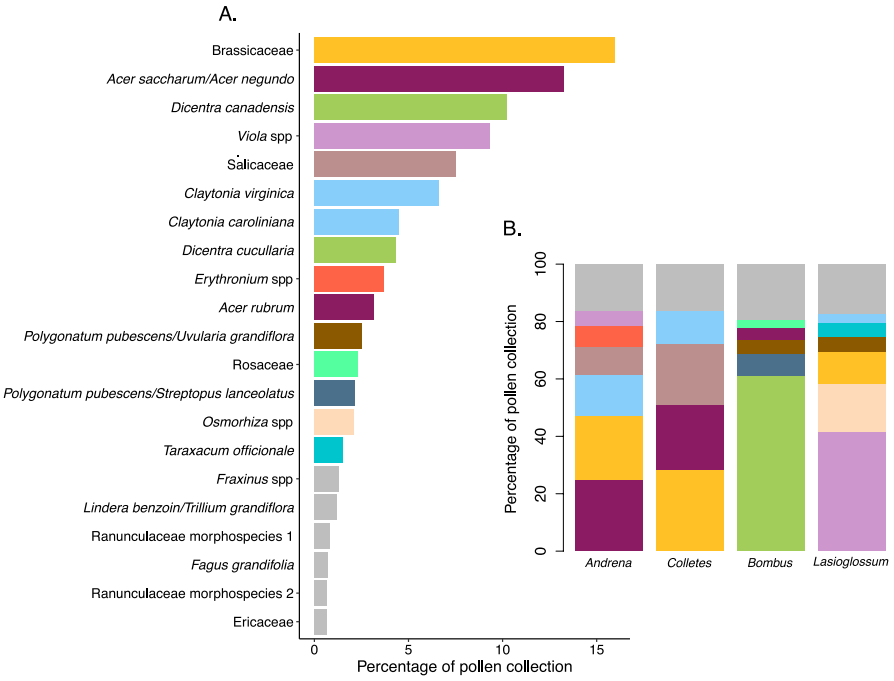

Fig. 3 **A**) The percentage of pollen collection by all bee specimens comprised by each pollen morphospecies; top 20 pollen morphospecies comprising 95% of overall pollen collection shown here. Morphospecies are color-coded by plant genus or family. **B**) For each bee genus represented by at least 50 specimens, the percentage of pollen collection comprised by each pollen morphogroup. Pollen morphospecies comprising the top 80% of pollen collected by each genus are displayed in color and are grouped and color-coded according to plant genus or family; those comprising the bottom 20% are in gray

from maples, and from willows. Specimens of *Bombus bimaculatus*, which comprised most *Bombus* specimens in the full pollen dataset, predominantly collected pollen from two species in the genus *Dicentra*, while specimens belonging to other *Bombus* species predominately collected pollen from and the spring herbs *Polygonatum pubescens* and *Streptopus lanceolatus,* and lesser amounts of pollen from *Taraxacum officionale*, *Viola* spp., and plants in the Rosaceae (Figure S3). Specimens of *Lasioglossum quebecense*, which comprised most *Lasioglossum* specimens in the full pollen dataset, predominantly collected pollen from spring ephemeral species in the genera *Viola* and *Osmorhiza* (Figure S4). Specimens of other *Lasioglossum* species also predominately collected pollen from *Viola* spp., as well as from plants in the Brassicaceae (Figure S4).

Collection of Pollen from Trees and Shrubs

In the full pollen dataset, bees collected pollen from 12 tree and shrub morphospecies which together comprised 29% of bees' overall pollen collection. Six of the top 20 pollen morphospecies were trees or shrubs, with the most pollen coming from maple species, willow species, and trees or shrubs in the family Rosaceae. The dominant bee genera differed in how much they collected pollen from trees or shrubs ($X^2 = 93.42$, df $= 3$, $p < 2.2 \times 10^{-16}$); 41% of pollen collection by *Andrena* came from trees or shrubs and 49% for *Colletes*, but only 12% for *Bombus* and 4% for *Lasioglossum* (Fig. 4; Table S5). All four bee genera collected pollen from maple and willow species, with *Andrena* also collecting pollen from an additional 7 tree and shrub taxa, including plants in the family Rosaceae, the genus *Fraxinus* (ash) and *Fagus grandifolia* (American beech).

Floral Visitation Versus Scopal Pollen Collection

We identified pollen in pollen samples from 13 plant taxa that we did not observe any specimens visiting. This included pollen from 10 tree and shrub morphospecies, many of which we were unable to observe bees' visits to directly because it is difficult to observe visits to tree flowers without tree-climbing equipment. Consequently, bee genera collected pollen from a wider breadth of plants than was indicated by visitation data alone. For each bee genus, 3–4 plant species comprised 80% of plant visitation while 4–8 pollen morphospecies comprised the top 80% of pollen collection (Fig. 5).

The combination of visitation and pollen collection data also revealed plants that, in many cases, are apparently visited more for nectar than for pollen. For example, for *Andrena* and *Colletes*, 36% and 28% of visits were to *Claytonia virginica*, but *Claytonia virginica* pollen comprised only 11% and 6.5% of the pollen collection of these genera, respectively (Fig. 5). Additionally, we observed bees visiting eleven plant species whose pollen we never found in pollen loads, though visits to these plants comprised only 2% of bees' visits overall (Tables S3-4).

Discussion

Broadleaf deciduous forest has been the dominant land cover of the Northeast and upper Midwestern United States since deglaciation in the early Holocene (Williams 2003; Faison et al. 2006; Raiho et al. 2022), suggesting that the native bee species associated with deciduous forest were historically dominant in this region prior to widespread deforestation following European colonization. Despite bees' co-evolutionary history with forest flora in these regions, there is little contemporary evidence about which floral resources bees use in mature deciduous forests or how to manage deciduous forests to conserve bee fauna. We documented bee associations with 60 plant species in total and we identified 18 plant taxa that serve as dominant floral resources for bee genera in mature deciduous forest habitats. Many of these plant species have previously been shown to rely on native bee species for pollination (Motten 1986; Motten et al. 1981; Parker et al. 2016; Edens-Meier et al. 2020; Beattie 1971; Macior 1978; Schemske et al. 1978). Our work here provides perspective on bees' use of the forest plant species to which they provide pollination, and with which they likely co-evolved. To our knowledge, these records constitute the largest and most spatially extensive source of data on bees' use of floral resources within mature deciduous forest habitat in North America. As such, they provide a useful reference point for conservation and restoration of forest bee-plant interactions.

We found that dominant forest bee genera differed in their use of plants, with some bee genera predominantly collecting pollen from a subset of understory herbs, while others stratified their pollen collection across canopy trees, shrubs, and a different subset of understory herbs (Figs. 2, 3, and 4). This outcome is consistent with the general consensus regarding bee foraging strategies, which is that bee taxa often differ in their use of floral resources, especially pollen (Cane and Sipes 2006; reviewed in Danforth et al. 2019), likely in part due to differences among bee taxa in nutritional needs (Vaudo et al. 2024; Roulston and Cane 2000). Indeed, the four dominant genera we compared differ strongly in body size and life history strategies, which have been suggested as contributing to differences between bee taxa in their nutritional needs and the types of flowers they are able to manipulate to extract resources (Portman et al. 2019; reviewed in Danforth et al. 2019).

Despite collecting all of our bee specimens from understory plants, which introduces a sampling bias against pollens from trees and shrubs, nearly one third of the pollen that bees carried came from trees or shrubs. Scopal loads of specimens in the genus *Andrena* and the species *Colletes inaequalis* were especially dominated by tree and shrub pollen, most of which came from maples and willows (Figs. 3 and 4, Figure S2). This is especially striking considering that we focused sampling in areas with relatively high understory floral abundance and diversity, where we might have expected understory resources to compose higher proportions of bee diets. The high use of tree and shrub pollen that we observed is consistent with recent, limited study of bee foraging in both eastern and western temperate forests that suggests that shrubs and trees are important resources for bees in temperate forests broadly. Regarding western temperate forests, a study

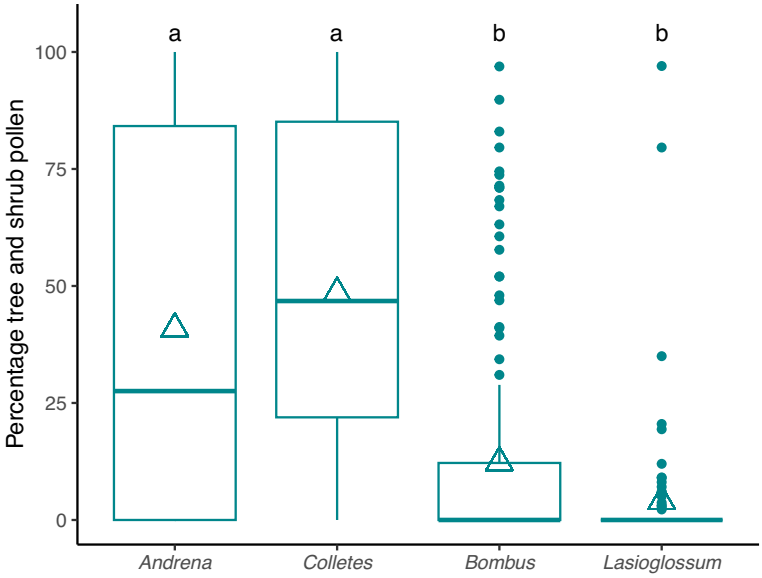

Fig. 4 Percentage of bees' scopal pollen comprised by tree and shrub pollen, for each bee genus. Boxplots show median percentages and the 25 th and 75 th quartiles of the data. Model-estimated mean percentages are indicated with triangles. We modelled the proportion of tree and shrub pollen in each scopal load as a function of bee genus using a generalized linear model with a binomial error structure. Statistically significant differences between genera, determined by post-hoc Tukey contrasts, are indicated by differing letters

published in this issue provides the first characterization of bee pollen foraging in western coniferous forests and shows high use of flowering shrubs by *Osmia lignaria* (Rivers et al. 2025). In the east, studies show many bee species in the Northeastern and upper-Midwestern United States depend on spring-flowering trees and shrubs for pollen and frequently forage in forest canopies (Russo and Danforth 2017; Wood et al. 2018; Wood and Roberts 2018; Smith et al. 2019; Urban-Mead et al. 2021, 2023; McLaughlin et al. 2022). Most of these previous eastern data, though, were collected in non-forest habitat, or otherwise in forests where bees did not have access to diverse understory floral resources. Thus, it was possible that previous data on spring-time foraging in the east was skewed by lack of herbaceous understory resources to show a higher extent of tree and shrub foraging. However, our findings add important contextualization by highlighting that even if bees have access to high quality floral resources in the forest understory, many species will still collect large quantities of pollen from tree species, including dominant canopy tree species such as sugar maples, as well as from woody plants such as willow species and plants in the Rosaceae. While a number of studies have now documented the vertical stratification of bee communities across in deciduous forests (McLaughlin et al. 2022; Urban-Mead et al. 2021; reviewed in Cunningham-Minnick et al. 2024), few have actually quantified the foraging activities of bees in canopies (but see Urban-Mead et al. 2023). More studies on bees' pollen collection that sample both in the canopy and in the

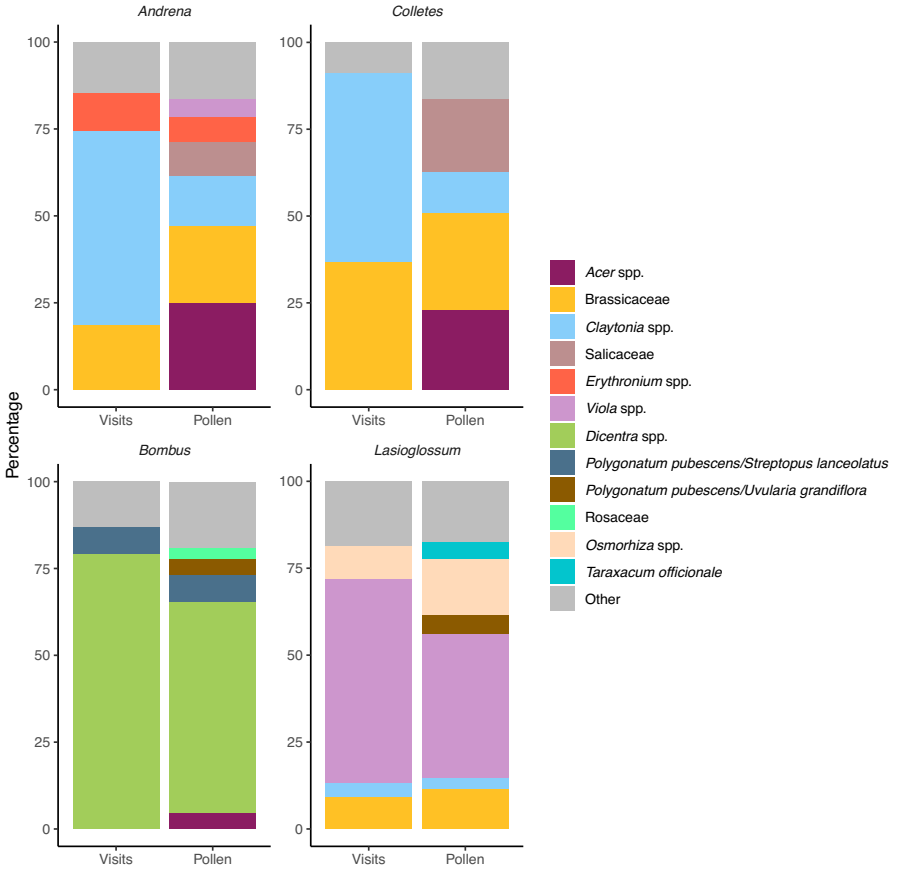

Fig. 5 Comparison of the percentage of visits with percent pollen collection. For the percentage of visits, plant species have been grouped according to pollen morphospecies. Plant taxa comprising 80% of a bee genus' visits or pollen collection are grouped and color-coded by plant genus, or in the case of Salicaceae, Brassicaceae and Rosaceae, plant family; those comprising the bottom 20% are denoted as "Other" and are in gray

understory are needed to provide a full picture of how forest bee communities are using canopy resources, particularly in forests where canopy sampling has not yet been done.

In addition to revealing use of canopy tree species and shrubs, pollen analysis also added nuance to a number of floral associations. Firstly, *Andrena* and *Colletes* were frequent visitors to spring beauties (*Claytonia virginica* and *C. caroliniana*), but collected relatively little spring beauty pollen, while their pollen collection from other plants they visited more closely resembles their visitation of those plants (Fig. 5, Figure S4). This contrast is consistent with previous work on generalist bee species' patterns of foraging on *Claytonia* populations in Pennsylvania, Maryland, and North Carolina, USA, and in Ontario, Canada (Parker et al. 2016, 2018; Smith et al. 2023), and could suggest that these bees primarily use *Claytonia* as a nectar resource in this

system. Given that spring beauty is regionally abundant in the temperate deciduous forest biome (Smith et al. 2023), *Claytonia* may play an important role supporting forest bees not only by providing pollen for its abundant specialist *Andrena erigeniae* (which we omitted from our analyses), but also by providing nectar as fuel for canopy and shrub foraging by other species. Secondly, one especially abundant species of *Andrena* in our samples, *Andrena erythronii*, is typically thought of as a pollen specialist on spring herbs in the genus *Erythronium*. However, *Erythronium* pollen only comprised 24% of pollen-collection by *A. erythronii*, and *A. erythronii* specimens collected pollen from 21 pollen morphospecies (Table S4). This consistent use of other pollen resources across study sites suggests that *A. erythronii*'s designation as a specialist on *Erythronium* may warrant revision. Finally, bees' high visitation to species of violets (*Viola canadensis*, *V. pubescens* and *V. sororia*) was surprising, as previous pollen analyses for spring bees have not documented violets as important resources, and violets are not generally considered to be particularly attractive to bees. We had initially assumed that the visits we observed must have been for nectar foraging, as bees are often thought to be less discerning in their choice of nectar than pollen. Pollen analysis showed, though, that bees in our study system, especially *Lasioglossum* specimens, are in fact using *Viola* sp. as a dominant pollen resource (Fig. 3).

While our study provides much needed information about which plants support native bee communities, our ability to guide management based on the floral associations we document here is still limited in several ways. Firstly, our data reflects bees' relative use of different plant resources in our study system, but does not address the degree to which bee demography in this system depends on these specific resources. Most of the floral resources that dominated bees' scopal loads were abundant at study sites and prevalent in the landscape. The pollen of these plant species may have been highly collected by bees merely because they were readily available, and not because they are actually preferred or nutritionally superior resources compared to the less abundant plants at study sites (Harmon-Threatt et al. 2017). Additionally, while we are able to make a broad comparison of highly-used floral resources collected by four dominant forest bee genera, our pollen data are skewed toward a small number of dominant bee species, and cannot provide an in-depth characterization of the pollen collection of most individual bee species in this system. While bee genera often exhibit differences in pollen use, bee species within the same genus can differ as well (Minckley and Roulston 2006; Danforth et al. 2019; Vaudo et al. 2024; Wood and Roberts 2017), and so understanding how management will affect bee communities will require more information on species-specific resource needs. Finally, the mature maple-dominated forest types we sampled represent a subset of temperate broadleaf deciduous forest types, and so the associations we document here may or may not be representative of the plants that are important resources for forest bees across different deciduous forest types and age classes. Studies that assess bee species' degree of preference for different floral resources across deciduous and coniferous forest types and age classes, and how these preferences relate to bee demography, are needed to further guide management.

The striking differences in foraging we observed among bee genera, though, broadly suggest that forest management that promotes plant diversity across forest

herb, shrub, and canopy layers is likely to support forest bee diversity in mature maple-dominated deciduous forests. This approach would be conceptually consistent with the dominant paradigm in biodiversity-centered forest management, which is that to conserve biodiversity and promote ecosystem resilience, management should promote canopy diversity and structural complexity of forests (Angelstam 1998; Long 2009; Raymond et al. 2009). Indeed, the few studies that have tested the effects of forest structural complexity or tree species diversity on bee communities have found positive effects (Traylor et al. 2024; Rappa et al. 2023; Eckerter et al. 2021). There is little data on how ecological forestry practices affect bee communities though, and studies have only occurred in the Southeastern United States and in Europe (Ulyshen et al. 2022; Chase et al. 2023; Traylor et al. 2024; Rappa et al. 2023; Eckerter et al. 2021). Thus, a fruitful future research direction would be to test how bee communities in Northeastern and upper-Midwestern forests respond to common practices in biodiversity-sensitive forest management. These include forest health practices such as deer culls and invasive species management which promote understory shrub and herb diversity (Aronson and Handel 2011; Bourg et al. 2017; Maynard-Bean and Kaye 2019; Moore et al. 2023; Boulanger et al. 2015; Haffey and Gorchov 2019), and, in forestry contexts, timber harvesting practices such as irregular shelterwoods and thinning, which encourage structural and compositional complexity while still maintaining mature forest cover (Raymond et al. 2009). In the absence of targeted studies that examine the effects of these practices, our results suggest that managing for a diversity of native forest plant species that are known to provide support across bee taxa will likely be beneficial.

Conclusions

Deciduous forest bees are a taxonomically and phenologically distinct group of bee species that likely dominated the bee fauna of the Northeastern and upper-Midwestern United States prior to widespread deforestation following European colonization. This study provides some of the first data on bee species' floral resource use in mature deciduous forest habitat with diverse understory communities. As such, it provides a useful reference point for more degraded deciduous forests that are subject to higher deer browse and invasive species. Our findings show that dominant forest bee genera exhibit divergent foraging behavior and thus greater plant diversity is likely important for supporting the forest bee community at large. In addition, we confirm that even in forest stands with diverse understory flowering plants, bees commonly collect pollen from canopy tree species and other woody plants. Future research on bees' pollen preferences in different forest contexts and under contrasting management types, as well as demographic studies that can link bee reproduction to aspects of nutrition in forested landscapes, are needed to best guide management of deciduous forests for bee communities.

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Authors' Contributions L.W. and R.W. conceived the study. L.W. collected and analyzed data and drafted the manuscript. L.W. and T.R. identified pollen. K.T. conducted molecular analyses to identify Viola sp. pollen. L.W., K.T. and R.W. revised the manuscript.

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Data Availability Data will be made available upon publication from the Dryad Digital Repository.

Declarations

Competing Interests The authors declare no competing interests.

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Authors and Affiliations

Lucia R. Weinman[1,2,3] · Katherine J. Turo[3] · Trent Ress[3] · Rachael Winfree[3]

✉ Lucia R. Weinman
luciaraew@gmail.com

[1] Graduate Program in Ecology & Evolution, Rutgers University, 14 College Farm Road, New Brunswick, NJ 08901, USA

[2] Present Address: Department of Entomology and Nematology, University of California, Davis, Davis, CA 95616, USA

[3] Department of Ecology, Evolution & Natural Resources, Rutgers University, New Brunswick, NJ 08901, USA

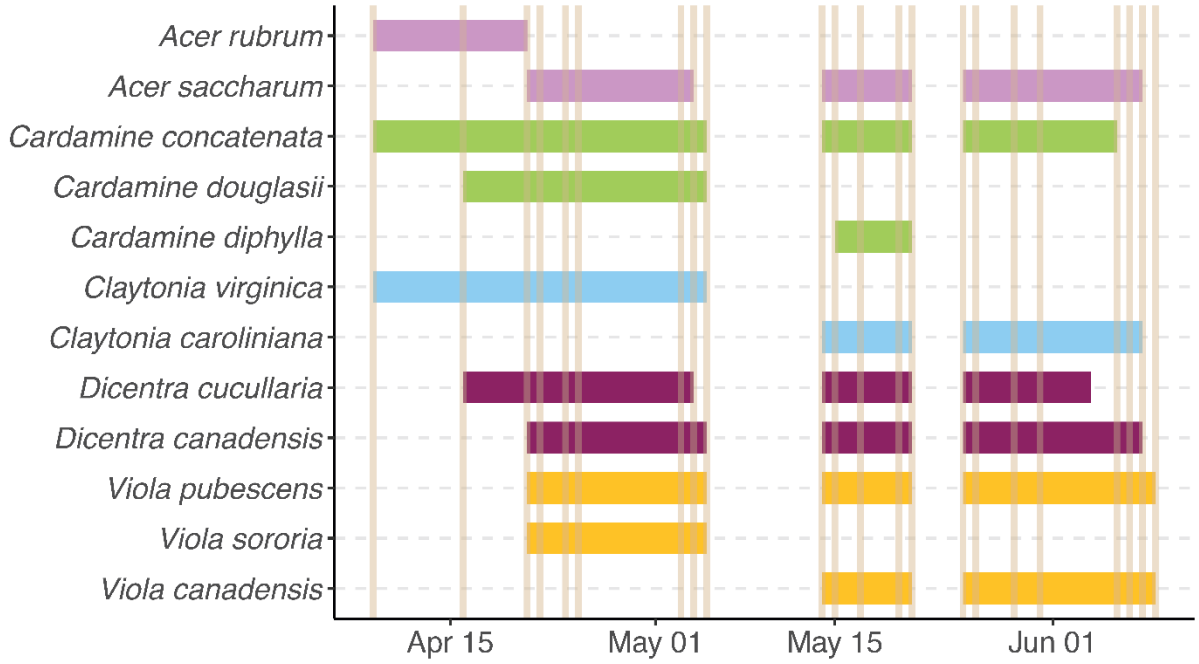

Figure S1. Gantt chart of flowering phenology for maple species and dominant spring herb species during the 2019 sampling period. Periods when plant species were observed to flower are indicated with horizonal bars; colors represent plant genera. Dates of data collection are indicated with vertical tan bars.

Methods S1. Deer and invasive plant management at study locations

The maple-dominated forests we sampled are actively managed by the National Park Service to mitigate pressures of invasive plant species and deer browse, though the specifics of management differ among forest stands and among parks.

Deer management

At Indiana Dunes National Park, the park service conducts deer culls throughout the park, In and around the Chellberg Farm area, where one of our sites was located, culls have occurred annually since 2013 (A. Derkacz, pers. comm.). Our other two sites at the park were located in two disconnected parcels, where the park service does not conduct deer culls. However, deer hunting is popular and occurs annually in the agricultural lands surrounding each of these parcels, and annual monitoring of the spring ephemeral herb species in the genus Trillium at one of these parcels showed low deer browse up to and during the time of our study (A. Derkacz, pers. comm.).

We also had one site at the Moraine Nature Preserve, a preserve managed by the Indiana Department of Natural Resources and located 5 km from our nearest site at Indiana Dunes National Park. The Indiana DNR began culling deer at this site in 2017, the year prior to our study (Calumet Collaborative et al. 2018).

At Sleeping Bear Dunes National Lakeshore, the park service does not conduct deer culls in the mainland portion of the park, but seasonal recreational deer hunting is permitted in the areas of the park that we sampled.

At Pictured Rocks National Lakeshore, the park service does not conduct deer culls, but seasonal recreational deer hunting is permitted. In a forest health assessment conducted the year

prior to our study, deer browse was found to be limited throughout the park, including in areas where we sampled (Sanders and Kirschbaum 2019).

Invasive species management

At Indiana Dunes National Park, the park service manages for the invasive herb garlic mustard (*Alliaria petiolata*) at several locations throughout the park, including in the area of one of our study sites (D. Robertson-Thompson, pers. comm.). Cover of garlic mustard was low at all of our study sites within the park (first author, pers. obs.). Cover of invasive shrubs varies (Hop et al. 2009), and was medium to low within our study sites (first author, pers. obs).

At Sleeping Bear Dunes National Lakeshore, the park service manages for the invasive forest understory herb garlic mustard throughout the park (NPS 2008); cover of garlic mustard and invasive shrubs are relatively low within the beech-maple forests at this park that were the focus of our study (Hop et al., 2011; first author pers. obs.). Invasive shrub cover was low (Hop et al. 2011; first author pers. obs.).

At Pictured Rocks National Lakeshore, the park service manages for the invasive herb forget-me-not (*Myosotis sylvaticus*). We did not observe forget-me-not at four of our five study sites within the park, but forget-me-not cover was high at the site we sampled in 2019 (first author, pers. obs.). We did not observe invasive shrubs at our study sites; no invasive shrubs were documented in a forest health survey conducted in beech-maple forests throughout the park, including in the areas where we sampled (Sanders and Kirschbaum 2019).

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Table S1. For each park and each study site, the total number of person hours of sampling and foraging bee specimens collected, and sample coverage for richness of bee species we detected, plant species we observed bees to visit, and pollen moprhospecies we observed in bees' scopal pollen loads.

Park	Site	Number of bee specimens	Number of person-hours	Sample coverage, bee species	Sample coverage, plant species visited	Sample coverage, pollen morphospecies
Indiana Dunes National Park		1683	98.5	0.993	0.999	0.980
	Pinhook Bog	590	22.9			
	Chellberg Farm	573	25.7			
	Heron Rookery	516	34.4			
	Moraine Preserve	493	15.5			
Sleeping Bear Dunes National Lakeshore		1144	42.4	0.989	0.999	0.978
	Shauger Hill Road	406	23.6			
	Pyramid Point	272	15.2			
	Burnham Road	243	18.3			
	Empire Bluffs	223	13.8			
Pictured Rocks National Lakeshore		874	58.2	0.984	0.998	0.976
	Chapel-Mosquito	293	19.3			
	Log Slide	244	16.7			
	Miners Road	210	5.0			
	Mosquito Falls	103	14.1			
	Chapel Rock	24	5.5			

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Table S2. Number of specimens of each bee species we collected in the visitation dataset, and for which we identified pollen from scopal loads. Note that specimens of *Andrena erigeniae* and the kleptoparasitic genus *Nomada* were deliberately omitted from pollen analysis.

Bee genus	Bee species	Number of specimens in visitation dataset	Number of specimens in pollen dataset
Agapostemon	*Agapostemon sericeus*	1	0
Andrena	*Andrena erigeniae*	527	0
	Andrena nasonii	245	37
	Andrena rugosa	204	109
	Andrena rufosignata	203	10
	Andrena carlini	200	51
	Andrena erythronii	154	105
	Andrena vicina	142	2
	Andrena cressonii	118	7
	Andrena geranii	79	0
	Andrena pruni	74	5
	Andrena nigrihirta	49	1
	Andrena nivalis	46	5
	Andrena forbesii	35	3
	Andrena barbilabris	27	0
	Andrena imitatrix	23	1
	Andrena alleghaniensis	21	1
	Andrena miserabilis	14	2
	Andrena dunningi	11	0
	Andrena illini	7	0
	Andrena perplexa	6	0
	Andrena arabis	5	0
	Andrena thaspii	5	0
	Andrena crataegi	3	0
	Andrena distans	3	0
	Andrena fenningeri	3	0
	Andrena milwaukeensis	2	1
	Andrena violae	2	0
	Andrena algida	1	0
	Andrena regularis	1	0
	Andrena salictaria	1	0
	Andrena spiraeana	1	0
	Andrena wilmattae	1	0
Anthophora	*Anthophora terminalis*	1	0

Apis	*Apis mellifera*	2	0
Augochlora	*Augochlora pura*	125	5
Augochlorella	*Augochlorella aurata*	46	4
Augochloropsis	*Augochloropsis metallica*	4	1
	Augochloropsis fulgida	1	0
Bombus	*Bombus bimaculatus*	212	138
	Bombus sandersoni	59	3
	Bombus impatiens	45	4
	Bombus ternarius	39	7
	Bombus perplexus	37	3
	Bombus vagans	32	2
	Bombus griseocollis	12	5
	Bombus terricola	2	0
	Bombus citrinus	1	0
	Bombus fernaldae/flavidus	1	0
Ceratina	*Ceratina calcarata*	44	0
	Ceratina mikmaqi	9	0
	Ceratina dupla	7	0
	Ceratina strenua	6	0
Colletes	*Colletes inaequalis*	213	59
	Colletes validus	2	1
Halictus	*Halictus confusus*	28	7
	Halictus rubicundus	12	0
Lasioglossum	*Lasioglossum quebecense*	138	52
	Lasioglossum subviridatum	124	7
	Lasioglossum cressonii	88	6
	Lasioglossum laevissimum	60	3
	Lasioglossum versans	43	0
	Lasioglossum coeruleum	41	1
	Lasioglossum cattellae	37	0
	Lasioglossum paraforbesii	35	0
	Lasioglossum leucozonium	28	2
	Lasioglossum nigroviridae	28	1
	Lasioglossum coriaceum	24	2
	Lasioglossum inconditum	23	1

	Lasioglossum oblongum	14	1
	Lasioglossum pilosum	12	3
	Lasioglossum gotham	10	0
	Lasioglossum obscurum	10	0
	Lasioglossum athabascense	8	1
	Lasioglossum planatum	7	1
	Lasioglossum acuminatum	6	1
	Lasioglossum leucocomus	6	1
	Lasioglossum lineatulum	6	0
	Lasioglossum birkmanni	5	0
	Lasioglossum pectorale	2	0
	Lasioglossum catellae cf. *"hemimelas"*	1	0
	Lasioglossum hitchensi	1	0
	Lasioglossum perpunctatum	1	0
Nomada	*Nomada bidentate group*	69	0
	Nomada luteoloides	53	0
	Nomada pygmaea	47	0
	Nomada imbricata	6	0
	Nomada cressonii	2	0
	Nomada denticulata	2	0
	Nomada composita	1	0
	Nomada depressa	1	0
	Nomada luteola	1	0
	Nomada sp.	1	0
Osmia	*Osmia bucephala*	35	1
	Osmia atriventris	20	1
	Osmia pumila	14	0
	Osmia cornifrons	13	1
	Osmia georgica	5	0
	Osmia lignaria	4	0
	Osmia taurus	3	0
	Osmia tersula	3	0
	Osmia sp.	1	0
Xylocopa	*Xylocopa virginica*	1	0

Table S3. The number of specimens of each bee species we collected from (or while visiting) each plant species.

Bee species	Plant species	Number of visits
Agapostemon sericeus	*Dicentra cucullaria*	1
Andrena algida	*Claytonia caroliniana*	1
Andrena alleghaniensis	*Cardamine diphylla*	7
	Viola pubescens	6
	Claytonia caroliniana	3
	Viola canadensis	3
	Carex spp	1
	Galium aparine	1
Andrena arabis	*Claytonia virginica*	3
	Cardamine concatenata	2
Andrena barbilabris	*Claytonia caroliniana*	21
	Cardamine concatenata	2
	Cardamine diphylla	1
	Claytonia virginica	1
	Taraxacum officinale	1
	Viola pubescens	1
Andrena carlini	*Claytonia virginica*	97
	Cardamine concatenata	65
	Viola pubescens	8
	Claytonia caroliniana	7
	Cardamine douglassii	4
	Sanguinaria canadensis	4
	Enemion biternatum	3
	Thalictrum thalictroides	2
	Viola canadensis	2
	Viola spp	2
	Anemone acutiloba	1
	Erigenia bulbosa	1
	Erythronium albidum	1
	Erythronium americanum	1
	Panax trifolius	1
	Taraxacum officinale	1
Andrena crataegi	*Claytonia virginica*	1
	Trillium grandiflorum	1

	Viola canadensis	1
Andrena cressonii	*Claytonia virginica*	103
	Cardamine concatenata	4
	Cardamine douglassii	3
	Enemion biternatum	3
	Ranunculus hispidus	2
	Erigenia bulbosa	1
	Thalictrum thalictroides	1
	Viola pubescens	1
Andrena distans	*Claytonia virginica*	1
	Erythronium albidum	1
	Erythronium americanum	1
Andrena dunningi	*Cardamine concatenata*	9
	Cardamine douglassii	1
	Claytonia virginica	1
Andrena erigeniae	*Claytonia virginica*	339
	Claytonia caroliniana	169
	Cardamine concatenata	6
	Viola pubescens	5
	Cardamine diphylla	2
	Cardamine douglassii	2
	Anemone acutiloba	1
	Aralia nudicaulis	1
	Erythronium albidum	1
	Viola canadensis	1
Andrena erythronii	*Claytonia caroliniana*	66
	Erythronium americanum	19
	Erythronium albidum	17
	Claytonia virginica	15
	Cardamine concatenata	13
	Viola pubescens	10
	Myosotis sylvatica	5
	Sanguinaria canadensis	4
	Anemone acutiloba	3
	Trillium grandiflorum	1
	Viola canadensis	1
Andrena fenningeri	*Claytonia virginica*	2
	Cardamine concatenata	1
Andrena forbesii	*Claytonia virginica*	21

	Claytonia caroliniana	5
	Cardamine concatenata	3
	Enemion biternatum	2
	Viola canadensis	2
	Anemone acutiloba	1
	Thalictrum thalictroides	1
Andrena geranii	*Cardamine diphylla*	55
	Viola pubescens	18
	Viola canadensis	3
	Taraxacum officinale	2
	Cardamine concatenata	1
Andrena illini	*Cardamine concatenata*	4
	Claytonia virginica	2
	Anemone acutiloba	1
Andrena imitatrix	*Claytonia virginica*	18
	Enemion biternatum	2
	Cardamine diphylla	1
	Lindera benzoin	1
	Trillium grandiflorum	1
Andrena milwaukeensis	*Myosotis sylvatica*	1
	Viola canadensis	1
Andrena miserabilis	*Claytonia virginica*	7
	Claytonia caroliniana	4
	Cardamine diphylla	1
	Cardamine douglassii	1
	Dicentra cucullaria	1
Andrena nasonii	*Claytonia virginica*	212
	Cardamine concatenata	14
	Enemion biternatum	5
	Erigenia bulbosa	4
	Anemone acutiloba	3
	Thalictrum thalictroides	3
	Claytonia caroliniana	1
	Panax trifolius	1
	Ranunculus hispidus	1
	Viola pubescens	1
Andrena nigrihirta	*Viola pubescens*	19
	Cardamine diphylla	9
	Viola canadensis	8

	Claytonia caroliniana	6
	Uvularia grandiflora	4
	Clintonia borealis	1
	Rubus pubescens	1
	Viola rostrata	1
Andrena nivalis	*Viola canadensis*	20
	Cardamine diphylla	11
	Viola pubescens	7
	Myosotis sylvatica	4
	Streptopus lanceolatus	2
	Claytonia caroliniana	1
	Claytonia virginica	1
Andrena perplexa	*Claytonia virginica*	5
	Enemion biternatum	1
Andrena pruni	*Claytonia virginica*	61
	Cardamine concatenata	6
	Trillium grandiflorum	3
	Caulophyllum thalictroides	1
	Dicentra cucullaria	1
	Viola pubescens	1
	Viola sororia	1
Andrena regularis	*Myosotis sylvatica*	1
Andrena rufosignata	*Claytonia caroliniana*	94
	Myosotis sylvatica	79
	Viola canadensis	12
	Viola pubescens	11
	Streptopus lanceolatus	4
	Cardamine diphylla	1
	Osmorhiza spp	1
	Uvularia grandiflora	1
Andrena rugosa	*Claytonia virginica*	84
	Claytonia caroliniana	49
	Cardamine concatenata	38
	Viola pubescens	12
	Uvularia grandiflora	7
	Cardamine diphylla	5
	Viola canadensis	3
	Anemone acutiloba	2

	Enemion biternatum	1
	Myosotis sylvatica	1
	Thalictrum thalictroides	1
	Trillium grandiflorum	1
Andrena salictaria	*Claytonia virginica*	1
Andrena spiraeana, stylopized	*Uvularia grandiflora*	1
Andrena thaspii	*Viola canadensis*	2
	Osmorhiza spp	1
	Rubus pubescens	1
	Streptopus lanceolatus	1
Andrena vicina	*Cardamine concatenata*	71
	Claytonia virginica	45
	Claytonia caroliniana	16
	Cardamine douglassii	3
	Trillium grandiflorum	3
	Anemone acutiloba	1
	Cardamine diphylla	1
	Myosotis sylvatica	1
	Streptopus lanceolatus	1
Andrena violae	*Viola canadensis*	1
	Viola sororia	1
Andrena wilmattae	*Claytonia virginica*	1
Anthophora terminalis	*Viola canadensis*	1
Apis mellifera	*Cardamine concatenata*	1
	Claytonia virginica	1
Augochlora pura	*Claytonia virginica*	73
	Enemion biternatum	11
	Viola canadensis	9
	Cardamine diphylla	8
	Viola pubescens	8
	Thalictrum thalictroides	4
	Myosotis sylvatica	2
	Ranunculus hispidus	2
	Cardamine concatenata	1
	Cardamine douglassii	1
	Claytonia caroliniana	1
	Dicentra canadensis	1
	Dicentra cucullaria	1
	Mitella diphylla	1

	Taraxacum officinale	1
	Trillium grandiflorum	1
Augochlorella aurata	*Viola pubescens*	30
	Claytonia virginica	8
	Viola spp	3
	Cardamine diphylla	1
	Claytonia caroliniana	1
	Enemion biternatum	1
	Floerkea proserpinacoides	1
	Thalictrum thalictroides	1
Augochloropsis fulgida	*Claytonia virginica*	1
Augochloropsis metallica	*Cardamine diphylla*	2
	Caulophyllum thalictroides	1
	Taraxacum officinale	1
Bombus bimaculatus	*Dicentra canadensis*	128
	Dicentra cucullaria	66
	Polygonatum pubescens	5
	Claytonia virginica	3
	Ribes cynosbati	2
	Trillium grandiflorum	2
	Uvularia grandiflora	2
	Aralia nudicaulis	1
	Cardamine concatenata	1
	Cardamine douglassii	1
	Viola pubescens	1
Bombus citrinus	*Claytonia virginica*	1
Bombus fernaldae/flavidus	*Viola canadensis*	1
Bombus griseocollis	*Dicentra canadensis*	3
	Dicentra cucullaria	3
	Cardamine concatenata	2
	Trillium grandiflorum	2
	Cardamine douglassii	1
	Enemion biternatum	1
Bombus impatiens	*Dicentra canadensis*	24
	Dicentra cucullaria	8
	Viola pubescens	3
	Cardamine diphylla	1

	Claytonia virginica	1
	Geranium maculatum	1
	Polygonatum pubescens	1
	Ribes cynosbati	1
	Streptopus lanceolatus	1
	Taraxacum officinale	1
	Thalictrum dioicum	1
	Trillium grandiflorum	1
	Uvularia grandiflora	1
Bombus perplexus	*Dicentra canadensis*	14
	Viola canadensis	11
	Dicentra cucullaria	5
	Streptopus lanceolatus	4
	Claytonia caroliniana	2
	Erythronium americanum	1
Bombus sandersoni	*Viola canadensis*	20
	Streptopus lanceolatus	13
	Dicentra canadensis	10
	Viola pubescens	6
	Dicentra cucullaria	5
	Myosotis sylvatica	3
	Cardamine diphylla	1
	Claytonia caroliniana	1
Bombus ternarius	*Streptopus lanceolatus*	24
	Viola canadensis	6
	Claytonia caroliniana	3
	Myosotis sylvatica	2
	Viola pubescens	2
	Dicentra canadensis	1
	Erythronium americanum	1
Bombus terricola	*Claytonia caroliniana*	2
Bombus vagans	*Viola canadensis*	14
	Polygonatum pubescens	11
	Streptopus lanceolatus	3
	Viola pubescens	3
	Claytonia caroliniana	1
Ceratina calcarata	*Claytonia virginica*	27
	Viola pubescens	6
	Cardamine concatenata	3

	Ranunculus hispidus	2
	Taraxacum officinale	2
	Viola canadensis	2
	Cardamine douglassii	1
	Trillium grandiflorum	1
Ceratina dupla	*Claytonia virginica*	3
	Cardamine diphylla	1
	Ranunculus hispidus	1
	Viola canadensis	1
	Viola pubescens	1
Ceratina mikmaqi	*Claytonia virginica*	7
	Cardamine concatenata	1
	Ranunculus hispidus	1
Ceratina strenua	*Claytonia virginica*	3
	Viola pubescens	2
	Thalictrum thalictroides	1
Colletes inaequalis	*Claytonia caroliniana*	136
	Claytonia virginica	35
	Cardamine concatenata	33
	Myosotis sylvatica	2
	Viola canadensis	2
	Anemone acutiloba	1
	Cardamine douglassii	1
	Dicentra canadensis	1
	Thalictrum thalictroides	1
	Viola pubescens	1
Colletes validus	*Claytonia caroliniana*	1
	Viola canadensis	1
Halictus confusus	*Viola pubescens*	10
	Cardamine diphylla	7
	Viola canadensis	5
	Claytonia caroliniana	2
	Cardamine concatenata	1
	Claytonia virginica	1
	Trillium grandiflorum	1
	Viola rostrata	1
Halictus rubicundus	*Viola canadensis*	6
	Claytonia virginica	4
	Dicentra cucullaria	1

	Viola pubescens	1
Lasioglossum acuminatum	*Dicentra cucullaria*	3
	Claytonia caroliniana	2
	Viola pubescens	1
Lasioglossum athabascense	*Viola canadensis*	6
	Claytonia caroliniana	1
	Dicentra cucullaria	1
Lasioglossum birkmanni	*Claytonia virginica*	3
	Floerkea proserpinacoides	2
Lasioglossum catellae ef. "hemimelas"	*Osmorhiza spp*	1
Lasioglossum cattellae	*Claytonia virginica*	15
	Cardamine concatenata	4
	Enemion biternatum	4
	Floerkea proserpinacoides	4
	Thalictrum thalictroides	3
	Cardamine douglassii	2
	Alliaria petiolata	1
	Anemone acutiloba	1
	Dicentra cucullaria	1
	Trillium grandiflorum	1
	Viola pubescens	1
Lasioglossum coeruleum	*Claytonia virginica*	20
	Claytonia caroliniana	5
	Cardamine concatenata	4
	Anemone acutiloba	3
	Dicentra cucullaria	2
	Viola pubescens	2
	Cardamine diphylla	1
	Dicentra canadensis	1
	Thalictrum thalictroides	1
	Viola canadensis	1
	Viola rostrata	1
Lasioglossum coriaceum	*Viola canadensis*	12
	Claytonia virginica	4
	Viola pubescens	4
	Cardamine diphylla	1

	Claytonia caroliniana	1
	Ranunculus hispidus	1
	Thalictrum thalictroides	1
Lasioglossum cressonii	*Viola pubescens*	29
	Viola canadensis	17
	Cardamine diphylla	16
	Claytonia virginica	8
	Ranunculus hispidus	5
	Taraxacum officinale	5
	Cardamine concatenata	2
	Enemion biternatum	2
	Floerkea proserpinacoides	2
	Galium aparine	1
	Sambucus racemosa	1
Lasioglossum gotham	*Claytonia virginica*	4
	Cardamine concatenata	2
	Anemone acutiloba	1
	Cardamine douglassii	1
	Dicentra cucullaria	1
	Uvularia grandiflora	1
Lasioglossum hitchensi	*Claytonia virginica*	1
Lasioglossum inconditum	*Viola canadensis*	8
	Viola pubescens	5
	Osmorhiza spp	4
	Myosotis sylvatica	3
	Cardamine concatenata	1
	Claytonia caroliniana	1
	Claytonia virginica	1
Lasioglossum laevissimum	*Sanguinaria canadensis*	24
	Anemone acutiloba	20
	Cardamine concatenata	5
	Claytonia virginica	5
	Cardamine douglassii	1
	Carex spp	1
	Enemion biternatum	1
	Ranunculus hispidus	1
	Thalictrum thalictroides	1
	Trillium grandiflorum	1

Lasioglossum leucocomus	*Viola pubescens*	5
	Claytonia caroliniana	1
Lasioglossum leucozonium	*Viola canadensis*	24
	Viola pubescens	3
	Myosotis sylvatica	1
Lasioglossum lineatulum	*Cardamine diphylla*	3
	Claytonia caroliniana	1
	Claytonia virginica	1
	Dicentra cucullaria	1
Lasioglossum nigroviridae	*Viola canadensis*	15
	Viola pubescens	6
	Claytonia virginica	4
	Osmorhiza spp	2
	Cardamine diphylla	1
Lasioglossum oblongum	*Viola canadensis*	5
	Osmorhiza spp	2
	Viola pubescens	2
	Cardamine concatenata	1
	Claytonia caroliniana	1
	Claytonia virginica	1
	Myosotis sylvatica	1
	Taraxacum officinale	1
Lasioglossum obscurum	*Claytonia virginica*	5
	Floerkea proserpinacoides	2
	Enemion biternatum	1
	Ranunculus hispidus	1
	Viola pubescens	1
Lasioglossum paraforbesii	*Dicentra cucullaria*	23
	Dicentra canadensis	8
	Viola pubescens	2
	Claytonia caroliniana	1
	Uvularia grandiflora	1
Lasioglossum pectorale	*Viola pubescens*	2
Lasioglossum perpunctatum	*Claytonia virginica*	1
Lasioglossum pilosum	*Cardamine diphylla*	4
	Viola canadensis	4
	Viola pubescens	2
	Dicentra canadensis	1

	Trillium grandiflorum	1
Lasioglossum planatum	*Viola canadensis*	3
	Osmorhiza spp	2
	Viola pubescens	2
Lasioglossum quebecense	*Viola canadensis*	43
	Viola pubescens	39
	Osmorhiza spp	15
	Claytonia caroliniana	13
	Cardamine diphylla	11
	Uvularia grandiflora	5
	Myosotis sylvatica	4
	Carex spp	2
	Dicentra canadensis	2
	Cardamine concatenata	1
	Dicentra cucullaria	1
	Ranunculus abortivus	1
	Taraxacum officinale	1
Lasioglossum subviridatum	*Claytonia virginica*	42
	Cardamine concatenata	13
	Cardamine diphylla	10
	Viola pubescens	9
	Floerkea proserpinacoides	8
	Claytonia caroliniana	5
	Enemion biternatum	5
	Viola canadensis	4
	Dicentra cucullaria	3
	Galium aparine	3
	Thalictrum thalictroides	3
	Viola sororia	3
	Anemone acutiloba	2
	Cardamine douglassii	2
	Dicentra canadensis	2
	Osmorhiza spp	2
	Alliaria petiolata	1
	Anemone quinquefolia	1
	Carex spp	1
	Caulophyllum thalictroides	1

	Lindera benzoin	1
	Sambucus racemosa	1
	Taraxacum officinale	1
	Viola spp	1
Lasioglossum versans	*Osmorhiza* spp	13
	Floerkea proserpinacoides	5
	Viola canadensis	5
	Claytonia virginica	3
	Enemion biternatum	3
	Viola pubescens	3
	Galium aparine	2
	Myosotis sylvatica	2
	Taraxacum officinale	2
	Mitella diphylla	1
	Ranunculus abortivus	1
	Ranunculus hispidus	1
	Thalictrum thalictroides	1
	Uvularia grandiflora	1
Nomada bidentate group	*Cardamine diphylla*	37
	Claytonia virginica	14
	Claytonia caroliniana	10
	Cardamine concatenata	3
	Viola canadensis	2
	Taraxacum officinale	1
	Thalictrum thalictroides	1
	Viola pubescens	1
Nomada composita	*Myosotis sylvatica*	1
Nomada cressonii	*Cardamine diphylla*	1
	Viola pubescens	1
Nomada denticulata	*Claytonia virginica*	1
	Enemion biternatum	1
Nomada depressa	*Myosotis sylvatica*	1
Nomada imbricata	*Claytonia virginica*	6
Nomada luteola	*Claytonia virginica*	1
Nomada luteoloides	*Claytonia virginica*	41
	Cardamine concatenata	9
	Anemone acutiloba	2
	Claytonia caroliniana	1

Nomada pygmaea	*Claytonia virginica*	37
	Cardamine douglassii	3
	Cardamine diphylla	2
	Claytonia caroliniana	2
	Cardamine concatenata	1
	Erythronium americanum	1
	Panax trifolius	1
Nomada sp. 2	*Claytonia caroliniana*	1
Osmia atriventris	*Claytonia virginica*	8
	Viola canadensis	6
	Viola pubescens	5
	Thalictrum thalictroides	1
Osmia bucephala	*Viola* spp	7
	Cardamine concatenata	6
	Viola sororia	6
	Dicentra canadensis	4
	Viola pubescens	4
	Claytonia virginica	3
	Erythronium americanum	2
	Dicentra cucullaria	1
	Erythronium albidum	1
	Viola canadensis	1
Osmia cornifrons	*Cardamine concatenata*	5
	Claytonia virginica	5
	Viola pubescens	3
Osmia georgica	*Claytonia virginica*	3
	Cardamine douglassii	2
Osmia lignaria	*Viola canadensis*	2
	Cardamine concatenata	1
	Claytonia virginica	1
Osmia pumila	*Claytonia virginica*	4
	Viola pubescens	4
	Viola canadensis	2
	Viola spp	2
	Cardamine concatenata	1
	Cardamine douglassii	1
Osmia sp.	*Viola pubescens*	1
Osmia taurus	*Claytonia virginica*	1
	Thalictrum thalictroides	1

	Viola pubescens	1
Osmia tersula	*Viola canadensis*	2
	Viola pubescens	1
Xylocopa virginica	*Cardamine douglassii*	1

Table S4. Pollen morphospecies data by bee genus. The "% pollen collection" refers to the percentage of all pollen collected by the bee genus comprised by each pollen morphospecies. The "Number of specimens" is the number of bee specimens that were carrying pollen of that morphospecies.

	Pollen morphospecies	% pollen collection	Number of specimens
Augochorella (4)	*Viola* spp.	78.4	4
	Lindera benzoin/Trillium grandiflora	10.7	2
	Asteraceae	5.1	1
	Brassicaceae	2.5	1
	Polygonatum pubescens/Uvularia grandiflora	2.3	1
	Fraxinus spp.	1.1	1
Augochlora (5)	*Claytonia virginica*	31.5	2
	Salicaceae	21.8	2
	Brassicaceae	18.2	1
	Ranunculaceae morphospecies 2	17.2	1
	Ranunculaceae morphospecies 1	9.1	2
	Unidentified 6	2.2	1
Augochloropsis (1)	Brassicaceae	100	1
Andrena (340)	Brassicaceae	21.6	146
	Acer saccharum/Acer negundo	19.8	130
	Claytonia virginica	11.0	100
	Salicaceae	9.3	106
	Erythronium spp.	7.2	58
	Claytonia caroliniana	5.8	63
	Viola spp.	4.8	45
	Acer rubrum	4.6	49
	Rosaceae	2.9	42
	Fraxinus spp.	2.5	17
	Lindera benzoin/Trillium grandiflora	1.4	21
	Polygonatum pubescens/Uvularia grandiflora	1.1	17
	Ranunculaceae morphospecies 1	1.1	14
	Fagus grandifolia	1.0	12
	Taraxacum officionale	1.0	16
	Polygonatum pubescens/Streptopus lanceolatus	1.0	4

	Myosotis sylvaticus	0.7	3
	Ranunculaceae morphospecies 2	0.7	11
	Aralia nudicaulis	0.5	10
	Betulaceae	0.3	15
	Unidentified	0.3	6
	Populus spp./*Juglans* spp.	0.2	3
	Unidentified 3	0.2	4
	Sanguinaria canadensis	0.2	7
	Erigenia bulbosa	0.2	6
	Ulmus spp.	0.1	1
	Osmorhiza spp.	0.1	2
	Maianthemum stellata/Maianthemum canadensis	0.1	1
Bombus	*Dicentra canadensis*	43.0	120
(162)	*Dicentra cucullaria*	18.2	81
	Polygonatum pubescens/Streptopus lanceolatus	6.9	12
	Polygonatum pubescens/Uvularia grandiflora	5.3	15
	Acer saccharum/Acer negundo	4.5	24
	Rosaceae	2.9	21
	Salicaceae	2.8	25
	Ericaceae	2.5	17
	Brassicaceae	1.8	9
	Taraxacum officionale	1.8	6
	Ribes cynosbati	1.6	5
	Unidentified	1.4	12
	Acer rubrum	1.1	6
	Viola spp.	0.9	7
	Lonicera canadensis	0.9	2
	Betulaceae	0.8	23
	Lindera benzoin/Trillium grandiflora	0.7	2
	Claytonia caroliniana	0.6	3
	Phlox divaricata	0.5	1
	Dicentra spp.	0.4	7
	Unidentified 4	0.3	1
	Ranunculaceae morphospecies 1	0.3	1
	Ranunculaceae morphospecies 2	0.2	2
	Unidentified 1	0.1	5
	Asteraceae	0.1	1
	Quercus spp.	0.1	3
	Unidentified 2	0.1	2
	Galium aparine/Lamiaceae	0.1	3

	Erigenia bulbosa	0.1	1
Colletes (60)	Brassicaceae	28.3	34
	Acer saccharum/Acer negundo	22.8	31
	Salicaceae	21.1	35
	Claytonia caroliniana	11.6	16
	Claytonia virginica	6.5	15
	Acer rubrum	4.3	16
	Viola spp.	3.4	3
	Ericaceae	1.2	1
	Betulaceae	0.3	4
	Dicentra cucullaria	0.2	2
	Polygonatum pubescens/Uvularia grandiflora	0.2	1
	Lindera benzoin/Trillium grandiflora	0.1	1
	Ranunculaceae morphospecies 2	0.1	1
Halictus (7)	*Viola* spp.	52.6	6
	Brassicaceae	29.0	3
	Ranunculaceae 456	6.7	1
	Dicentra canadensis	5.2	1
	Dicentra cucullaria	4.5	1
	Rosaceae	1.1	1
	Claytonia caroliniana	0.9	1
Lasioglossum (83)	*Viola* spp.	41.6	58
	Osmorhiza spp.	16.5	18
	Brassicaceae	11.5	15
	Polygonatum pubescens/Uvularia grandiflora	5.5	11
	Taraxacum officionale	4.8	5
	Claytonia caroliniana	3.0	8
	Lindera benzoin/Trillium grandiflora	2.3	5
	Sanguinaria canadensis	1.9	2
	Ranunculaceae morphospecies 2	1.7	3
	Fagus grandifolia	1.6	7
	Myosotis sylvaticus	1.4	4
	Aralia nudicaulis	1.2	2
	Acer rubrum	1.1	2
	Ribes cynosbati	1.0	1
	Dicentra canadensis	0.9	4
	Salicaceae	0.8	7
	Claytonia virginica	0.8	3
	Unidentified	0.8	2
	Rosaceae	0.6	4

Osmia (3)	*Carex* spp.	0.5	2
	Unidentified 3	0.2	2
	Fraxinus spp.	0.1	2
	Dicentra cucullaria	0.1	1
	Viola spp.	53.1	2
	Claytonia virginica	24.1	3
	Rosaceae	6.0	1
	Acer saccharum/Acer negundo	5.7	1
	Salicaceae	4.3	1
	Taraxacum officionale	4.0	1
	Galium aparine/Lamiaceae	2.7	1

Table S5. Results of pairwise Tukey contrasts comparing proportion of tree and shrub pollen collected by dominant bee genera, using the full pollen dataset.

Contrast	Estimate	Std. Error	z value	Pr(>|z|)
Colletes - Andrena	0.310	0.280	1.107	0.268
Bombus - Andrena	-1.598	0.263	-6.077	7.36 x 10-9
Lasioglossum - Andrena	-2.819	0.573	-4.918	1.30 x 10-6
Bombus - Colletes	-1.908	0.352	-5.416	1.83 x 10-7
Lasioglossum - Colletes	-3.130	0.619	-5.053	8.69 x 10-7
Lasioglossum - Bombus	-1.222	0.612	-1.997	0.055

Table S6. Results of PERMANOVA of scopal pollen carried by dominant bee genera in the reduced pollen dataset. Dominant bee genera differed in the composition of their scopal pollen.

pseudo-R^2	0.11
F	9.28
p	0.001

Table S7. Results of pairwise Tukey contrasts comparing proportion of tree and shrub pollen collected by dominant bee genera, using the reduced pollen dataset. The proportion of tree and shrub pollen was modelled as a function of bee genus identity using logistic regression (X^2=37.31, df = 3, p= 6.03×10^{-7}).

Contrast	Estimate	Std. Error	z value	Pr(>|z|)
Colletes - Andrena	0.482	0.313	1.540	0.148
Bombus - Andrena	-1.502	0.664	-2.260	0.036
Lasioglossum - Andrena	-3.117	1.161	-2.684	0.015
Bombus - Colletes	-1.984	0.691	-2.872	0.012
Lasioglossum - Colletes	-3.598	1.176	-3.059	0.012
Lasioglossum - Bombus	-1.615	1.314	-1.229	0.219

Figure S2. The percentage of pollen collection comprised by each pollen morphogroup for all Andrena specimens, the overrepresented species *Andrena erythronii* and *Andrena rugosa,* respectively, and for all specimens of all other Andrena spp. Pollen morphospecies comprising the top 80% of pollen collected by each genus are displayed in color and are color-coded according to plant genus or family; those comprising the bottom 20% are in gray.

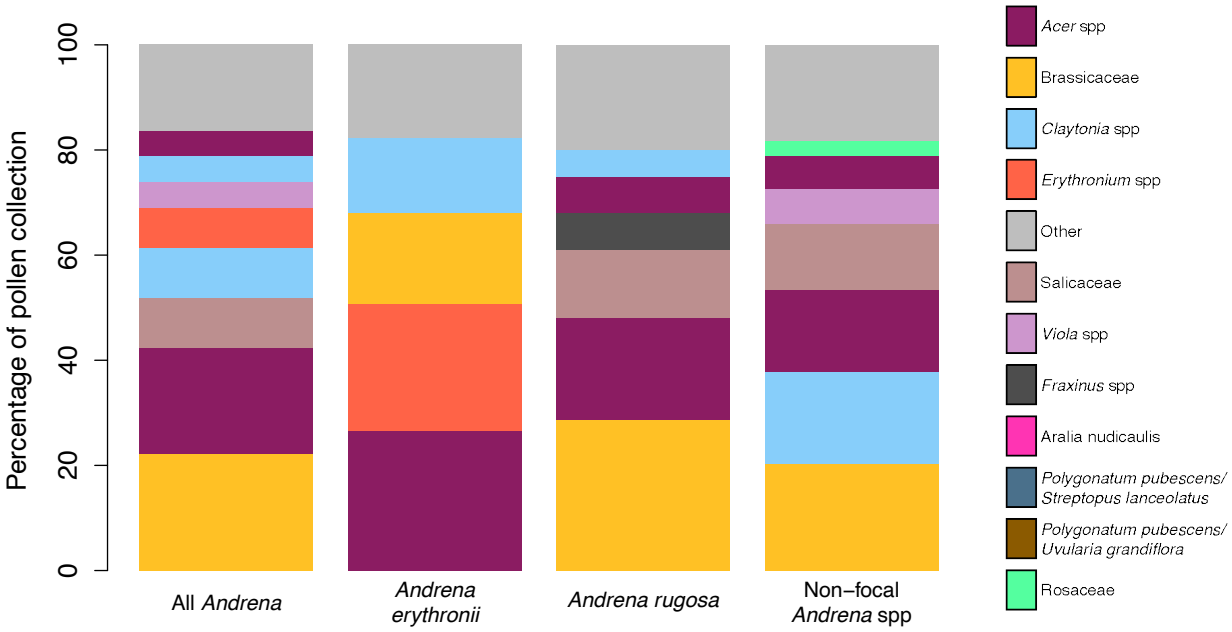


Figure S3. The percentage of pollen collection comprised by each pollen morphogroup for all *Bombus* specimens in the full pollen dataset, the overrepresented species *Bombus bimaculatus,* and for all specimens of *Bombus* spp. in the reduced pollen dataset. Pollen morphospecies comprising the top 80% of pollen collected by each genus are displayed in color and are color-coded according to plant genus or family; those comprising the bottom 20% are in gray.

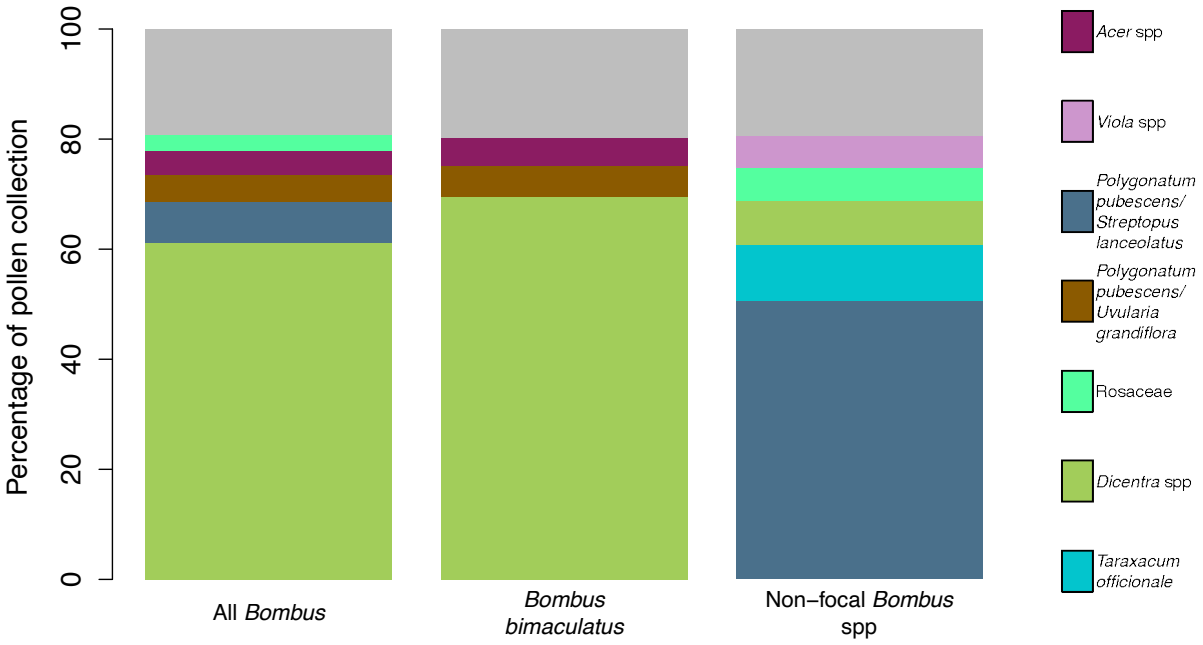


Figure S4. The percentage of pollen collection comprised by each pollen morphogroup for all *Lasioglossum* specimens, the overrepresented species *Lasioglossum quebecense,* and for all specimens of all other *Lasioglossum* spp. Pollen morphospecies comprising the top 80% of pollen collected by each genus are displayed in color and are color-coded according to plant genus or family; those comprising the bottom 20% are in gray.

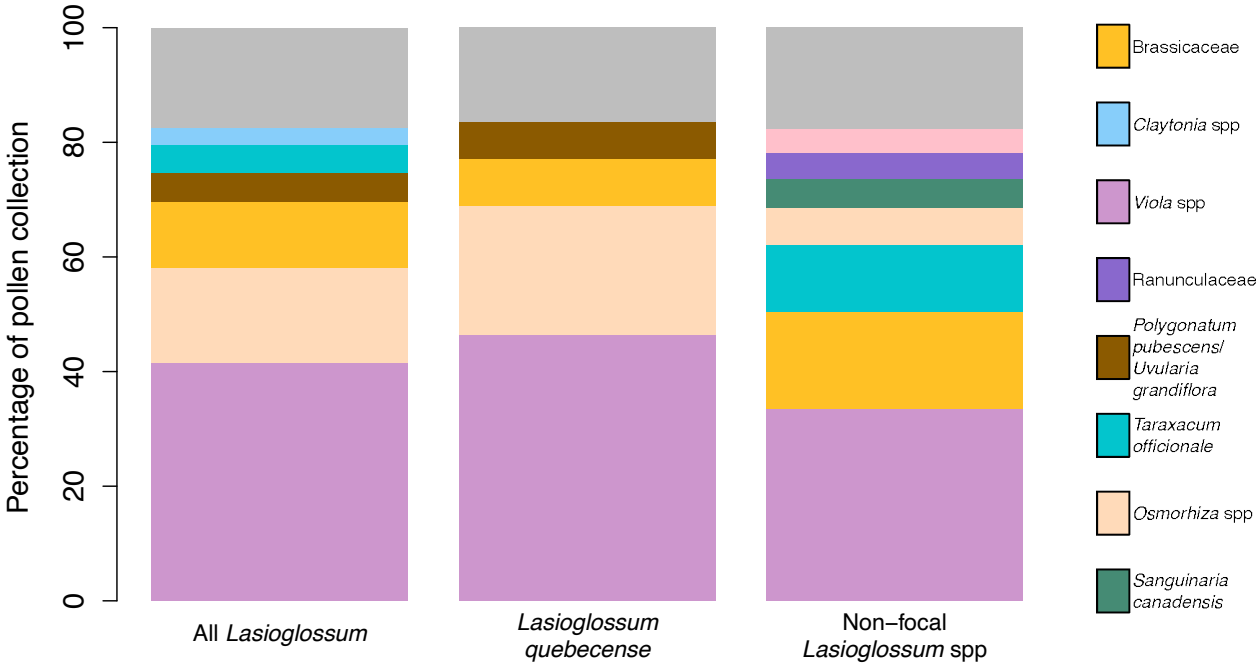
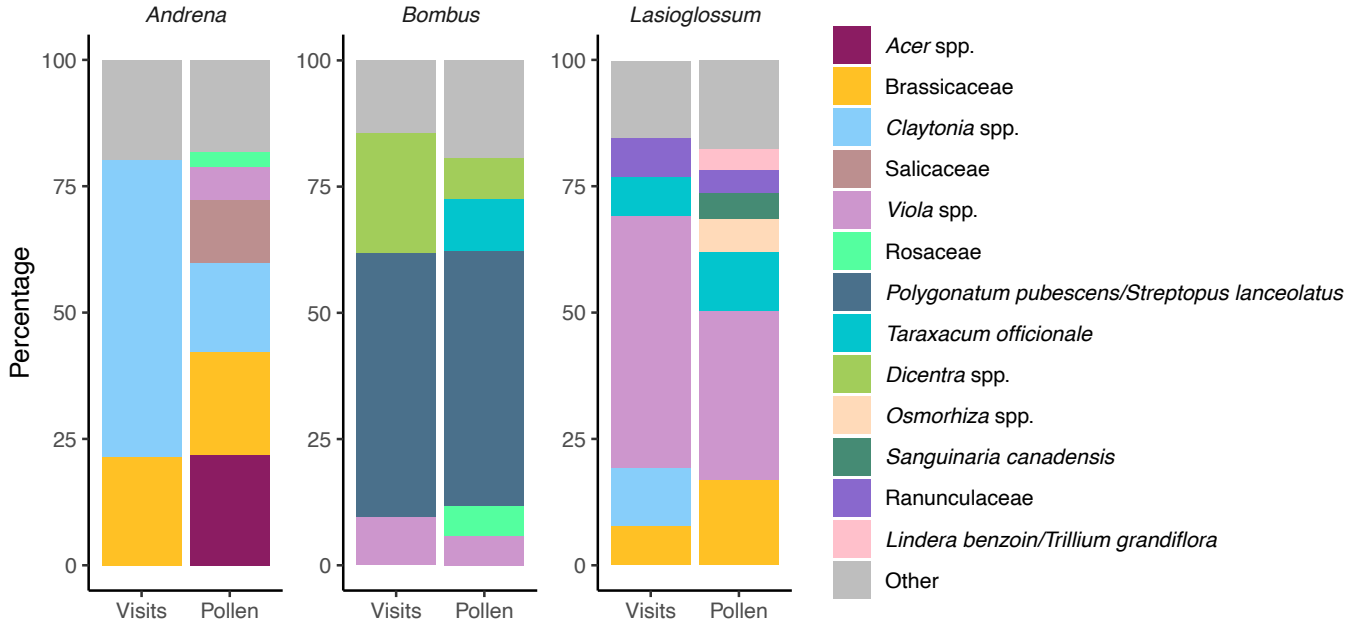


Figure S5. Comparison percentage of visits with percent pollen collection, for all specimens excluding *Andrena carlini*, *Andrena erythronii*, *Andrena nasonii*, *Andrena rugosa*, *Bombus bimaculatus*, and *Lasioglossum quebecense*. For the percentage of visits, plant species have been grouped according to pollen morphospecies. Plant taxa comprising 80% of a bee genus' visits or pollen collection are color-coded by plant genus, or in the case of Salicaceae, Brassicaceae and Rosaceae, plant family; those comprising the bottom 20% are denoted as "Other" and are in gray.



Methods S3. Molecular pollen identification

We were unable to resolve the identity of one morphospecies of highly abundant pollen in our samples through microscopic palynology and instead used a molecular analysis to determine the pollen species identity. We isolated and sequenced DNA from five representative samples that contained 88-100% of the unknown pollen type.

For each sample, we transferred pollen into a 250ul solution of 1% SDS within a screw cap microtube and filled the tube 2/3 with 1mm Zirconia beads. We lysed the pollen grains for 5 minutes at 2400 rpm in a Mini Bead beater-96 (BioSpec). Following Gouker et al., 2020, we used an acetone-based DNA extraction. We transferred 100ul from our bead beating tubes, pelleted the pollen coat and proteins with an 8-10m centrifuge cycle at 14,000 rpm, and transferred all supernatant into a 1:1 acetone wash under the hood. After vortexing and waiting one minute, pollen samples were centrifuged an additional minute at 6000 rpm and the supernatant was discarded. Pollen pellets were air-dried under the hood for 2 minutes to allow residual acetone to evaporate and then were resuspended in water.

We amplified the nuclear ribosomal ITS2 gene region using a published primer set (Chen et al. 2010) and a Phire Plant Direct PCR kit with standard conditions, 40 cycles, and an annealing temperature of 55.4 °C. Then, all samples were sequenced with a SeqStudio Genetic Analyzer at the Genomics Center sequencing core at Rutgers University, and subsequently identified using BLAST (NCBI GenBank). We filtered BLAST results for all sequences with >70% query coverage and >90% alignment for species identification. We then report the reference sequence with the lowest e-value.

Results

We identified all sequences as *Viola canadensis* (see Table S4). Our molecular identification is supported by our field observations as *V. canadensis* was one of four violet species present at our sites (*V. canadensis, V. pubescens, V. rostrata, V. sororia*), and we commonly observed bees foraging on *V. canadensis*. A third line of evidence comes from our morphological pollen analysis. In our initial analysis, our unknown pollen morphospecies was tricolporate, as expected for violets, although not all samples fully resembled our reference slides. This is not uncommon for violets, for which a third of known species contain heteromorphic pollen and for which interspecific hybridization occurs frequently (Marcussen et al. 2022).

Literature Cited

Chen S, Yao H, Han J, et al (2010) Validation of the ITS2 Region as a Novel DNA Barcode for Identifying Medicinal Plant Species. PLoS One 5:e8613. https://doi.org/10.1371/journal.pone.0008613

Gouker FE, Guo Y, Pooler MR (2020) Using acetone for rapid PCR-amplifiable DNA extraction from recalcitrant woody plant taxa. Appl Plant Sci 8:2–5. https://doi.org/10.1002/aps3.11403

Marcussen T, Ballard HE, Danihelka J, et al (2022) A Revised Phylogenetic Classification for Viola (Violaceae). Plants. https://doi.org/10.3390/plants11172224

Table S8. Query coverage, percent identity, and plant species identified by BLAST results for each pollen sample from which DNA was extracted and sequenced. The *'% unknown pollen'* refers to the percentage of grains in the pollen sample that were originally identified via microscopy as the unknown pollen morphospecies. '*Query coverage'* is the percentage of the unknown sample's sequence length that is included in the alignment against the known sequence (here, *Viola canadensis*). *'% identity'* is the percentage of identical nucleotides found at the same positions in both aligned sequences and indicates the degree of similarity between the unknown sample and known plant species.

Sample UID	Bee species	% Unknown Pollen	Plant species	Query Coverage	% Identity
1646	*Lasioglossum quebecense*	100%	*Viola canadensis*	85%	90.4%
1766	*Andrena nigrihirta*	100%	*Viola canadensis*	87%	90.2%
1820	*Bombus perplexus*	100%	*Viola canadensis*	91%	99.4%
1857	*Lasioglossum quebecense*	100%	*Viola canadensis*	96%	96.5%
4315	*Andrena erythronii*	88%	*Viola canadensis*	85%	95.3%