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# Bumble bee banquet: Genus- and species-level floral selection by Midwestern *Bombus*

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## Abstract

Regionally specific flower preference data are needed to optimize conservation habitat plantings for at-risk pollinators such as bumble bees (*Bombus* spp.). Current tools for selecting flowers for plantings rely on raw bee flower visits, which can be biased toward abundant flowers. To assist in planning habitat enhancements for bumble bees, we quantified genus- and species-level floral preferences using a selection index that accounts for floral availability. Through 477 h of observation in Ohio, USA during the summers of 2017 and 2018, we recorded 22,999 observations of eight *Bombus* species visiting 96 flowering plant taxa. As a genus, *Bombus* selected flowers nonrandomly; the most strongly preferred plants included *Asclepias* spp., *Cirsium* spp., Convolvulaceae, *Dipsacus* spp., *Echinacea purpurea*, *Monarda fistulosa*, *Penstemon digitalis*, and *Silphium* spp. Only a few Fabaceae were highly selected (*Baptisia* spp., *Trifolium pratense*, and *Vicia* spp.), while some were preferred only during their peak bloom (*Securigera varia*), and others were not preferred by bumble bees (*T. hybridum* and *Melilotus* spp.). Diets differed among habitats, and in restored meadows, bumble bees selected for native planted species such as *Monarda fistulosa*, *Asclepias syriaca*, *Echinacea purpurea*, *Penstemon digitalis*, and *Silphium* spp. Diets and preferences shifted over the season, largely driven by changes in plant phenologies (e.g., in June, *Penstemon* was strongly selected, in July, *Asclepias*, and in August, *Verbena*). For the three most common *Bombus* (*B. impatiens*, *B. griseocollis*, and *B. bimaculatus*), rarefaction analysis indicates that we were able to detect almost all plants in their summer diets. However, for five less common species, even our extensive sampling was insufficient to fully characterize their diets. The common *Bombus* species differed in their feeding niches, perhaps reducing interspecific competition. In contrast, we found high diet overlap between three rarer species—*B. vagans*, *B. fervidus*, and *B. pensylvanicus*, suggesting that these at-risk species might benefit from different floral communities than would the common species. Five of eight species

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(including one that is currently under review for federal listing) most strongly preferred one or another non-native plant, presenting managers with a conservation conundrum concerning how to balance the needs of bees with the preservation of native plants.

**KEYWORDS**
bee foraging, diet breadth, floral preference, floral selection, pollinator conservation, pollinator habitat, selection index, species niche overlap, statewide survey

## INTRODUCTION

Ongoing reductions in the amount and quality of pollinator habitat worldwide underlie urgent efforts to improve habitats for pollinating insects, particularly bees (Dicks et al., 2015, 2016; Kennedy et al., 2013; M'Gonigle et al., 2015; Williams et al., 2015). Especially worrisome are declines in the populations of key crop pollinators, such as the bumble bees, in many parts of the globe (Goulson et al., 2015; Tscharntke, 2021; Williams et al., 2009; Winfree et al., 2009). In the United States, recent bumble bee (*Bombus* spp.) population trends indicate some species are expanding and others are in steep decline (Cameron et al., 2011; Colla & Packer, 2008; Colla et al., 2012; Grixti et al., 2009). These findings warrant habitat initiatives focused on providing basic needs for bumble bees including undisturbed nesting and overwintering sites, as well as abundant and preferred floral resources that are free of pesticides (Carvell et al., 2007; Kovács-Hostyánszki et al., 2017). For some pollinators, such as specialist bees or monarch butterflies that have life cycle stages dependent on specific plant resources, choices of plant species for habitat improvements are straightforward (Belsky & Joshi, 2018; Fowler, 2016). For other species, including generalist bees, the choices for managers can be overwhelming.

Considering pollinator preferences, or floral use in relation to availability, is the next step in optimizing conservation plantings to target bumble bees or other taxa of interest. Information on bumble bee floral use is blossoming because of a recent surge in large-scale surveys (e.g., Butler et al., 2021; MacPhail et al., 2019; Novotny et al., 2021; Richardson et al., 2018; Wood et al., 2019) and in bee–flower association data from community science websites (e.g., iNaturalist, Bumble Bee Watch, USGS Bee Lab Ask a Bumble Bee Program). Models (M'Gonigle et al., 2017; Scheper et al., 2015; Williams et al., 2015) and other tools (e.g., Bumble Bee Flower Finder, https://bumblebeeflowerfinder.info; Sabatino et al., 2021) have also been developed to help managers pick appropriate flower species that support diverse bees. Unfortunately, these tools typically rely on raw observations of floral use, producing incomplete conclusions of floral preference that do not consider the effects of flower availability on bee use. Accounting for flower availability would enhance these tools by indicating plant species preferred by bees independent of flower abundance (Cole et al., 2020; Simanonok et al., 2021). Selection indices, which assess use in proportion to the abundance of resource types (Johnson, 1980), are useful to evaluate resource preferences under field conditions in which individual bees experience many floral choices that vary in abundance and distribution. Selection indices have contributed information about preferred diets of bumble bees in the Sierra Nevada mountains of California, USA (Cole et al., 2020), native bees in planted hedge rows within California agricultural landscapes (Morandin & Kremen, 2013), and honey bees and wild bees in the upper Midwestern states (Simanonok et al., 2021). These advances present opportunities to fine-tune conservation-oriented pollinator habitat plantings to benefit target species.

Bumble bees are generalist foragers that visit many plant species (Goulson, 2010) and utilize a variety of natural and managed foraging habitats. Bumble bees adjust their foraging choices to exploit the best of available resources in a particular time and place (Heinrich, 1979; Pyke, 1980; Raine & Chittka, 2007). Flower abundance, morphology, and reward increase visitation and fidelity of individual bumble bees (Goulson & Darvill, 2004; Harder, 1985). Seasonally, shifts in diet are necessary because the long duration of the colony life cycle exceeds the blooming period of most flower species (e.g., Fussell & Corbet, 1992). Foraging choices may also reflect the colony demand for pollen or nectar, itself a function of colony ontogeny and floral environment (Crone & Williams, 2016; Lanterman & Goodell, 2018; Malfi et al., 2022; Roulston & Goodell, 2011). Interspecific or intraspecific competition for flowers may further influence flower choice (Brian, 1957; Heinrich, 1976; Inoue et al., 2008).

Despite being floral generalists, bumble bee diet preferences vary substantially across species (e.g., Goulson & Darvill, 2004; Harder, 1985; Lundberg & Ranta, 1980; Wood et al., 2021), suggesting that one floral assemblage may not be best for all species. Further assessment of diet

niche overlap in natural habitats is needed to determine the extent to which species' realized floral use and inherent preferences overlap. Including bee preference (used here to indicate disproportionate use of a floral species relative to abundance) in the criteria for choosing species for conservation plantings should result in habitat that better promotes target bee taxa and could allow tailoring the mix regionally for at-risk bee species (Cole et al., 2020). Ideally, floral mixes could benefit multiple bee species of conservation interest. On a practical level, considering diet niche overlap of rare species with each other and with common species could further improve conservation value of a planting. Diverse plantings offer something for each species, but no simple formula for flower mixes that promotes rare species has emerged.

To assist in the planning of habitat enhancements for bumble bees, particularly at-risk species, we quantified bumble bee floral use and floral availability in natural and managed bee foraging habitats in the Midwestern United States, to determine which flower species are selected for or against the genus and species levels. To assess the impact of pollinator plantings on bumble bee diets, we compared indices of flower selection between habitats, focusing on the difference in bee flower selection between planted pollinator habitat versus other habitats. Specifically, we asked: (1) Do bumble bees use flowers in proportion to their availability or do they forage selectively? (2) Which plants are most strongly selected or avoided by bumble bees? (3) How does bumble bee floral use and selection differ among habitats, particularly in managed pollinator habitat compared with unmanaged habitats? (4) How does bumble bee flower selection vary across the growing season? (5) How do bumble bee species differ in their flower preferences? This paper focuses on bumble bee species' foraging patterns in natural habitats of the Midwestern United States, but the approach is applicable to other pollinators and locations (Cole et al., 2020; Simanonok et al., 2021).

# METHODS

## Study sites

We conducted 318 90-min surveys of bumble bees (*Bombus* spp.) and wildflowers at 228 locations in Ohio, USA, during June, July, and August in 2017 and 2018 (the time of peak annual bumble bee foraging activity). Study sites consisted of flower-rich patches of foraging habitat greater than 0.4 ha (mean 9.0 ± 15.2, max 134.4 ha) that were at least 2 km apart. Based on their vegetation and management, sites were classified as: natural field (unmanaged naturally regenerating herbaceous fields, such as recently abandoned croplands, $n = 63$), shrubby old field (unmanaged fields undergoing woody succession, with shrubs and small trees; $n = 45$), planted restored meadow (established meadow planted with abundant pollinator-friendly wildflowers, managed as pollinator habitat; $n = 149$), planted urban patch (patches of high-quality pollinator forage plants in urban settings, such as around nature centers; $n = 12$), roadside (highway and secondary road margins dominated by non-natives, especially Fabaceae, mowed regularly; $n = 34$), planted restored roadside (highway exit ramp infields planted as in restored meadows; $n = 10$), or planted hayfield (seeded with low diversity mix of *Trifolium* spp. and/or *Medicago sativa*, and harvested annually; $n = 5$). For further details on site selection, see Novotny et al. (2021).

## Bumble bee field surveys

Bee surveys were performed between the hours of 09:00 and 18:00 on clear weather days above 21°C. Upon each site visit, a team of one to four trained observers recorded bee visits to flowers for a total of 90 person-minutes. We searched the best available foraging habitat systematically and moved between flower patches often to minimize double-counting of individuals. Species identity and the flowering plant species on which each bee was observed were recorded for all *Bombus*. In the second year, social caste (male, worker, and gyne) of each bumble bee was also recorded. Observations were not categorized as pollen versus nectar visits. To minimize our impact and because of the large number of bumble bees observed at some sites (as many as 452 in a single survey), the majority were not collected. Instead most bumble bees were identified on the wing, or temporarily detained for identification following Colla et al. (2011). For two similar species, *B. auricomus* and *B. pensylvanicus*, some observers who were not able to distinguish them on the wing lumped them as *B. auricomus*/*B. pensylvanicus* undetermined to avoid lethally collecting sensitive species. These 156 individuals were excluded from analyses.

## Flower abundance field surveys

Upon each site visit, we estimated the available flower resources for bees along four 25 × 1 m transects (100 $m^2$ total area). The transects were haphazardly placed within the site to intersect the areas where bees were surveyed. In each transect, we recorded the number of flower units of each species in bloom, up to 1000 flower units per 25-m transect. Flower units were defined in "bee walkable clusters" (Saville, 1993) based on floral morphology and

observations of bee foraging behavior. What constituted a flower unit was defined separately for each plant species, but consistently across observers. Plants were identified using a field guide (Newcomb, 1989) or were photographed for later identification. Taxonomic names of plants follow the USDA PLANTS database (United States Department of Agriculture, Natural Resources Conservation Science, 2022). Flower abundance and bee visit data were aggregated among species within the following taxa due to inconsistency in species-level identification across observers (alphabetically): *Coreopsis* spp., *Dipsacus fullonum* with *D. laciniatus*, *Helianthus* spp. (excluding *H. annuus*), *Liatris* spp., *Polygonum cespitosum* with *P. persicaria*, other *Polygonum* spp., *Pycnanthemum tenuifolium* with *P. virginianum*; *P. incanum* with *P. muticum*; *Rosa* spp., *Rubus* spp., *Rudbeckia hirta* with *R. subtomentosa* and *R. fulgida*, *Silphium* spp., *Solidago* spp., *Stachys* spp., *Vernonia* spp., and *Vicia* spp.

## Data analysis

All analyses were conducted using the R programming language, version 3.6.3 (R Core Team, 2020).

In order to test the hypothesis that bees forage selectively and do not use flowers simply in proportion to their abundance, we compared matrices of use versus availability with a Mantel test (mantel function, Bray–Curtis distance with 999 permutations, "vegan" package, R; Oksanen et al., 2020). If there was no underlying correlation between bee use and flower availability per survey (indicated by a nonsignificant Mantel test), we concluded that bees actively sought out certain high-value flower species and avoided others.

In order to determine whether sampling effort was sufficient to capture the diet of all *Bombus* species, an accumulation curve was plotted for the number of plant species used by each bee species as the number of individual bees observed increased (rarecurve function, "vegan" package, R).

Bumble bee flower selection was measured with the selection ratio index (Manly et al., 2002; Savage, 1931). To calculate the selection index for each plant species, we first defined use as the proportion of total bumble bee visits that were to flowers of plant species *I* and availability as the proportion of flowering units of species *I* out of total flower abundance. Only plant taxa with more than five total bumble bee visit observations were included in flower abundance totals. Selection ratios for each plant taxon were then calculated as $\text{use}_i$ divided by $\text{availability}_i$ following Cole et al. (2020). Selection was considered positive if the proportion of use exceeded availability ($\text{use}_i/\text{availability}_i > 1$), in which case the selection $\text{index}_i = \text{use}_i/\text{availability}_i$. If $\text{use}_i/\text{availability}_i$ was less than 1 (negative selection) then selection $\text{index}_i = -1 \times ([\text{use}_i/\text{availability}_i]^{-1})$. Thus, a selection ratio of 2 indicates that bees used a plant species twice as often as expected based simply on plant abundance, and a selection ratio of −2 indicates that bees used a plant species half as often as expected.

Herein, we present selection ratios from aggregated data. However, see Appendix S1: Table S1 for mean site-level selection indices. For all plant species, variability (SD) greatly exceeded the mean, reducing our ability to interpret the mean site-level selection indices. Aggregating the data across sites also allowed us to calculate the selection index for those plant species that had values of 0 or "undefined" at the site level, because it allowed us to pool bee visits observed to those plant species at all sites. Selection index was not defined for 94 plant taxa that received zero or very few (1–4) total bumble bee visits (listed in Appendix S1: Table S2). Selection index was also not defined for 12 plant taxa that did receive more than five total *Bombus* visits, but were observed during bee surveys only and not captured by floral abundance transect surveys (Appendix S1: Table S1).

To visualize selection for or against flower species used by *Bombus* in our dataset, bumble bee floral use was plotted against floral availability. Outliers in percentage of total *Bombus* visits or percentage of total flower abundance were determined according to the interquartile range (IQR) rule, with values deemed outliers if they were at least 1.5 × IQR above the threshold for the third quartile or below the threshold for the first.

We generated lists of preferred bumble bee food plants that could be useful for restoration practitioners. To help minimize bias toward preferences of the dominant bee species, we constrained these lists by additional criteria (the number of bumble bee species that used a plant and the number of sites at which the plant and bee species co-occurred) before ranking plant taxa by selection index values.

To address the question of how bumble bee diets and flower selection differed between restored meadows versus other habitats, an adonis PERMANOVA test with pairwise comparisons was used to evaluate the significance of differences in site-level bumble bee flower use by habitat (pairwise.adonis2 function with 999 permutations and Bray–Curtis distance, "pairwiseAdonis" package, R; Arbizu, 2017). Permutational similarity percentages (SIMPER) analysis was used to generate a list of the flower taxa that contributed the most to differences in *Bombus* diets (explained the first 75% of cumulative variation in flower use) between restored meadows versus other habitats (simper function with 999 permutations, "vegan" package, R).

In order to assess the hypothesis that the strongly selected flower species changed within a season in

response to turnover in blooming plants, we calculated an adonis PERMANOVA test with pairwise comparisons by month.

We tested the hypothesis that diets differed among bumble bee species using an adonis PERMANOVA test of flower use by bee species, as described above. We also compared the mean rarefied niche overlap between all pairs of bee species. To account for differences in species' abundances on niche size (abundant species likely will be observed on more plant species than will rare species), the total visits per species were rarefied to 20 randomly resampled individuals per species 1000 times (rrarefy function, "vegan" package, R). For each randomly resampled community, niche overlap between species pairs was calculated as the Schoener index (niche.overlap function, "spaa" package, R; Zhang, 2016), a measure of the probability of sharing flower species based on the proportional use of each flower that ranges from 0 (no overlap) to 1 (complete overlap). Niche overlap was then averaged across the 1000 iterations.

To determine the extent to which each species' duration of annual activity influenced its diet, we calculated a Pearson correlation between diet breadth and activity span (first minus last growing degree day observed in June–August surveys). We assessed rarefied diet breadth as the mean ± SD number of plant taxa used per species in 1000 randomly resampled communities rarefied to 20 individuals per species (similar to Connop et al., 2010; Wood et al., 2021).

## RESULTS

### Do bumble bees use flowers in proportion to their availability or forage selectively?

We recorded 22,999 observations of eight bumble bee (*Bombus*) species visiting 96 flowering plant taxa, not including plant or bee species with fewer than five total visits or any bees that were not identified to species.

There was no overall association between the availability of flowers and their use by bumble bees (Mantel test for correlation of Bray dissimilarity between site-level *Bombus* flower use vs. availability matrices, $R = 0.010$, $p = 0.163$). This lack of correlation suggests that bumble bees selected flowers nonrandomly and preferred some plant species while avoiding others. Therefore, we investigated spatial (by habitat), seasonal (by month), and taxonomic (by species) trends in bumble bee flower preference via the selection ratio index.

Accounting for floral availability, not just use, greatly changed interpretations about which plant species are most preferred by bumble bees (Figure 1). We found no correlation between total selection index and percent *Bombus* visits to plant taxa ($t = 0.73$, df $= 82$, $p = 0.47$, $r = 0.08$). Of the top 10 plant species based on selection ratio, only two were also in the top 10 for use (Figure 2; *Dipsacus* spp. and *Asclepias syriaca*). The three biggest drops in rank were for *Securigera varia*, *Lotus corniculatus*, and *Ratibida pinnata*—all three were in the top 10 for raw use but dropped in rank by 55 or more places when their high abundance was accounted for using selection index (all were among the five most abundant flowers; Appendix S1: Table S1).

### Which plants are most strongly selected or avoided by the genus *Bombus*?

Bumble bees strongly selected and avoided some plant species out of proportion to their abundance (Table 1; Figure 1). Among plants that attracted five or more bee species, the most strongly selected by the genus *Bombus* were (with selection index values in the upper 75% quantile): *Cirsium vulgare*, *Veronicastrum virginicum*, *Dipsacus* spp., *Asclepias syriaca*, *Silphium* spp., *Calystegia sepium*, *Monarda fistulosa*, and *Convolvulus arvensis* (Table 1). Others that were positively selected relative to their abundance included *Echinacea purpurea*, *Baptisia alba*, and *Asclepias tuberosa*. Although Fabaceae were used by diverse *Bombus* species, the majority of plants in the overall bottom 25% quantile of selection index values were members of that family (*Desmodium* spp., *Lotus corniculatus*, *Melilotus alba*, *M. officinalis*, *Securigera varia*, and *Trifolium hybridum*).

Plant species that were found in >10% of flower abundance surveys on which we observed fewer than five bumble bee visits were: *Erigeron annuus* ($n_{\text{surveys}} = 243$ out of 318 surveys, $n_{\text{bee}} = 4$ *Bombus* visits), *Leucanthemum vulgare* ($n_{\text{surveys}} = 117$, $n_{\text{bee}} = 4$), *Achillea millefolium* ($n_{\text{surveys}} = 81$, $n_{\text{bee}} = 3$), *Medicago lupulina* ($n_{\text{surveys}} = 61$, $n_{\text{bee}} = 1$), and *Oxalis stricta* ($n_{\text{surveys}} = 41$, $n_{\text{bee}} = 1$) (Appendix S1: Table S2).

### How does bumble bee floral use and selection differ among habitats, particularly in managed pollinator habitat compared with unmanaged habitats?

*Bombus* diets in almost all habitat types were distinct ($F = 3.911$, df $= 6$, $p = 0.001$; Appendix S1: Table S3), at least in part because habitats differed in flower availability (adonis PERMANOVA, $F = 1.613$, df $= 6$, $p = 0.001$; Appendix S1: Table S4). *Bombus* flower use in restored meadows differed significantly from that

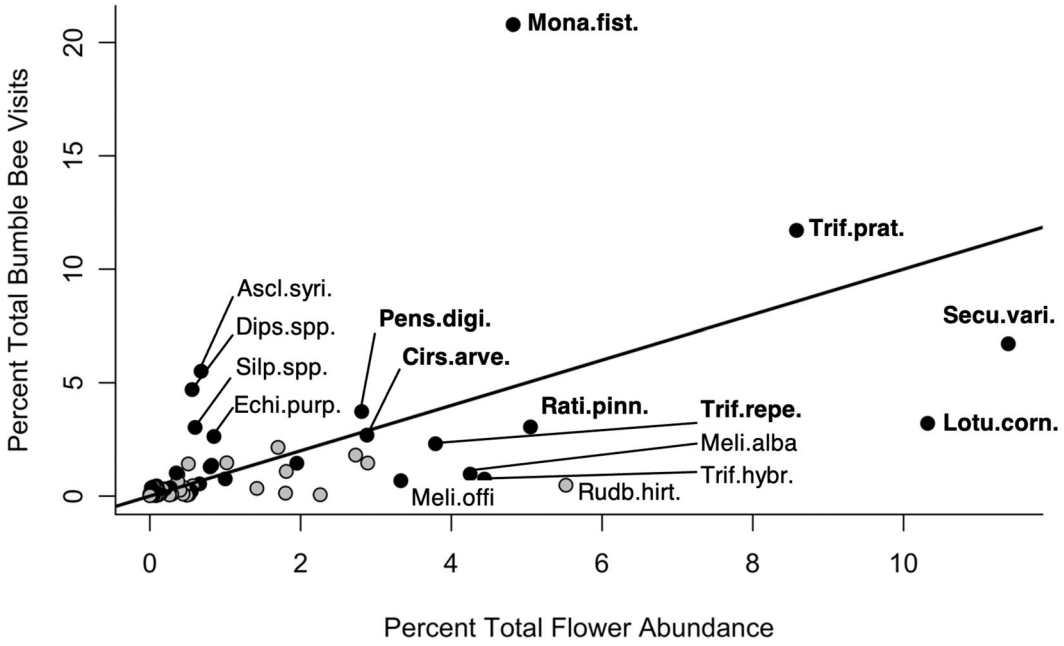



**FIGURE 1** Bumble bee use versus availability of food plants. Use is the percentage of total aggregated bumble bee visits, and availability is the percentage of total flower abundance. Black circles indicate plant species that were visited by five or more *Bombus* species, and gray circles fewer than five. The black line indicates a hypothetical 1:1 relationship in which bumble bees use flowers in direct proportion to their availability. Labeled plant species are outliers according to the interquartile rule for percentage of *Bombus* visits, percentage of flower abundance, or both (in boldface). Ascl.syri., *Asclepias syriaca*; Cirs.arve., *Cirsium arvense*; Dips.spp., *Dipsacus fullonum/laciniatus*; Echi.purp, *Echinacea purpurea*; Lotu.corn., *Lotus corniculatus*; Meli.alba, *Melilotus alba*; Meli.offi, *Melilotus officinalis*; Mona.fist., *Monarda fistulosa*; Pens. digi., *Penstemon digitalis*; Rati.pinn., *Ratibida pinnata*; Rudb.hirt, *Rudbeckia hirta*; Secu.vari., *Securigera varia*; Silp.spp., *Silphium* spp.; Trif. hybr., *Trifolium hybridum*; Trif.prat., *T. pratense*; Trif.repe., *T. repens*.



**FIGURE 2** Bumble bees visiting two flowering plants that ranked highly in both selection index value and raw use: a native milkweed (*Asclepias syriaca*, left; photo credit: Randall Mitchell) and an invasive teasel (*Dipsacus fullonum*, right; photo credit: Jessie Novotny).

**TABLE 1** Selection for food plants that attracted five or more bumble bee species.

| Plant species | Family | Selection ratio | No. surveys | No. *Bombus* species | Percentage of *Bombus* visits | | Percentage of flower abundance |
|---|---|---|---|---|---|---|---|
| | | | | | Common | Rare | |
| *Cirsium vulgare* | Asteraceae | 18.5 | 18 | 5 | 0.38 | 0.20 | 0.02 |
| *Veronicastrum virginicum*[a] | Scrophulariaceae | 14.5 | 6 | 5 | 0.29 | 0.20 | 0.02 |
| *Dipsacus* spp.[b] | Dipsacaceae | 8.4 | 61 | 8 | **4.71** | **4.58** | 0.56 |
| *Asclepias syriaca*[a] | Asclepiadaceae | 8.1 | 63 | 6 | **5.85** | 0.54 | 0.68 |
| *Silphium* spp.[a] | Asteraceae | 5.1 | 24 | 7 | **3.18** | 0.74 | 0.60 |
| *Calystegia sepium* | Convolvulaceae | 5.0 | 32 | 7 | 0.42 | 0.94 | 0.09 |
| *Monarda fistulosa*[a] | Lamiaceae | 4.3 | 95 | 8 | **20.81** | **20.40** | **4.82** |
| *Convolvulus arvensis* | Convolvulaceae | 3.8 | 18 | 5 | 0.40 | 0.13 | 0.10 |
| *Echinacea purpurea*[a] | Asteraceae | 3.1 | 75 | 6 | **2.74** | 1.15 | 0.85 |
| *Baptisia alba*[a] | Fabaceae | 3.0 | 5 | 6 | 0.10 | 0.81 | 0.05 |
| *Asclepias tuberosa*[a] | Asclepiadaceae | 2.9 | 36 | 5 | 1.08 | 0.20 | 0.35 |
| *Nepeta cataria* | Lamiaceae | 2.7 | 2 | 5 | 0.17 | 0.47 | 0.07 |
| *Prunella vulgaris* | Lamiaceae | 1.7 | 102 | 5 | 1.25 | **2.96** | 0.82 |
| *Vicia* spp. | Fabaceae | 1.6 | 14 | 7 | 1.23 | **2.15** | 0.80 |
| *Helianthus* spp.[a] | Asteraceae | 1.6 | 19 | 5 | 0.33 | 0.20 | 0.20 |
| *Liatris* spp.[a] | Asteraceae | 1.4 | 22 | 5 | 0.39 | 0.13 | 0.27 |
| *Trifolium pratense*[a] | Fabaceae | 1.4 | 177 | 8 | **10.57** | **28.42** | **8.58** |
| *Penstemon digitalis*[a] | Scrophulariaceae | 1.3 | 35 | 7 | **3.48** | **7.34** | **2.81** |
| *Cirsium arvense* | Asteraceae | −1.1 | 126 | 7 | **2.74** | **2.02** | **2.88** |
| *Lathyrus latifolius* | Fabaceae | −1.2 | 3 | 5 | 0.22 | 0.34 | 0.26 |
| *Cichorium intybus* | Asteraceae | −1.2 | 75 | 6 | 0.53 | 0.74 | 0.66 |
| *Apocynum cannabinum* | Apocynaceae | −1.3 | 58 | 5 | 0.79 | 0.34 | 1.00 |
| *Heliopsis helianthoides*[a] | Asteraceae | −1.3 | 66 | 5 | 1.54 | 0.20 | 1.95 |
| *Trifolium repens*[a] | Fabaceae | −1.6 | 132 | 6 | **2.34** | **1.75** | **3.79** |
| *Ratibida pinnata*[a] | Asteraceae | −1.7 | 84 | 6 | **3.22** | 0.54 | **5.05** |
| *Securigera varia* | Fabaceae | −1.7 | 73 | 8 | **6.79** | **5.79** | **11.39** |
| *Verbena hastata*[a] | Verbenaceae | −2.5 | 34 | 6 | 0.20 | 0.54 | 0.55 |
| *Lotus corniculatus* | Fabaceae | −3.2 | 111 | 5 | **3.01** | **6.13** | **10.32** |
| *Desmodium* spp. | Fabaceae | −4.3 | 24 | 5 | 0.12 | 0.13 | 0.51 |
| *Melilotus alba* | Fabaceae | −4.4 | 74 | 6 | 1.01 | 0.47 | **4.25** |
| *Melilotus officinalis* | Fabaceae | −4.9 | 91 | 5 | 0.68 | 0.74 | **3.33** |
| *Trifolium hybridum*[a] | Fabaceae | −5.9 | 134 | 7 | 0.72 | 1.14 | **4.44** |

*Note*: *Bombus* flower preference was evaluated by selection ratio index (quantiles shown with horizontal lines) based on total aggregated data. Plants that attracted more than half of *Bombus* species observed in our dataset are shown here (for all plants, see Appendix S1: Table S1). *Bombus* species is the total number of bumble bee species observed visiting that plant species. Percentage of common *Bombus* visits is the percentage of visits to each plant out of the total aggregated *B. impatiens*, *B. griseocollis*, and *B. bimaculatus* observations. Percentage of rarer *Bombus* visits is the percentage of visits to each plant out of the total aggregated *B. vagans*, *B. fervidus*, *B. perplexus*, *B. auricomus*, and *B. pensylvanicus* observations. Percentage of flower abundance was out of aggregated total data (values in boldface exceeded 1.5 × interquartile range). Horizontal lines mark quartile ranges of selection index value.

[a]Species commonly seeded at pollinator habitat restoration sites in Ohio.

[b]Invasive in Ohio according to the Ohio Department of Agriculture.

in all other habitats. On the other hand, flower use in unmanaged early successional fields did not differ significantly from that in two other unimproved habitats (roadsides and shrubby successional old fields) (Appendix S1: Table S4). Plant species that contributed the most to cumulative differences in diets between

improved bee foraging habitat (sites with large plantings managed to support pollinators) versus other habitats included a mix of preferred native forage plants (*Asclepias syriaca*, *Echinacea purpurea*, *Monarda fistulosa*, *Penstemon digitalis*, and *Silphium* spp.), as well as weedy species in the Fabaceae family (*Securigera varia* and *Trifolium pratense*), and non-native plants (*Cirsium arvense* and *Dipsacus* spp.) (Appendix S1: Table S5). Others not on that list of highly influential species in *Bombus* diets that were nonetheless strongly selected in managed pollinator habitat plantings were (alphabetically): *Asclepias* spp., *Gaillardia pulchella*, *Helianthus* spp., *Senna hebecarpa*, and *Veronicastrum virginicum* (Figure 3). *Rudbeckia hirta* and *Coreopsis* spp. had the lowest bumble bee selection index values among restoration plants.

## How does bumble bee flower selection vary across the growing season?

Total *Bombus* diet shifted significantly among the months of June, July, and August (adonis PERMANOVA test of site-level bee flower use by month $F = 6.515$, $df = 2$, $p = 0.001$, each month distinct according to post hoc pairwise comparisons). In each month, the plants with

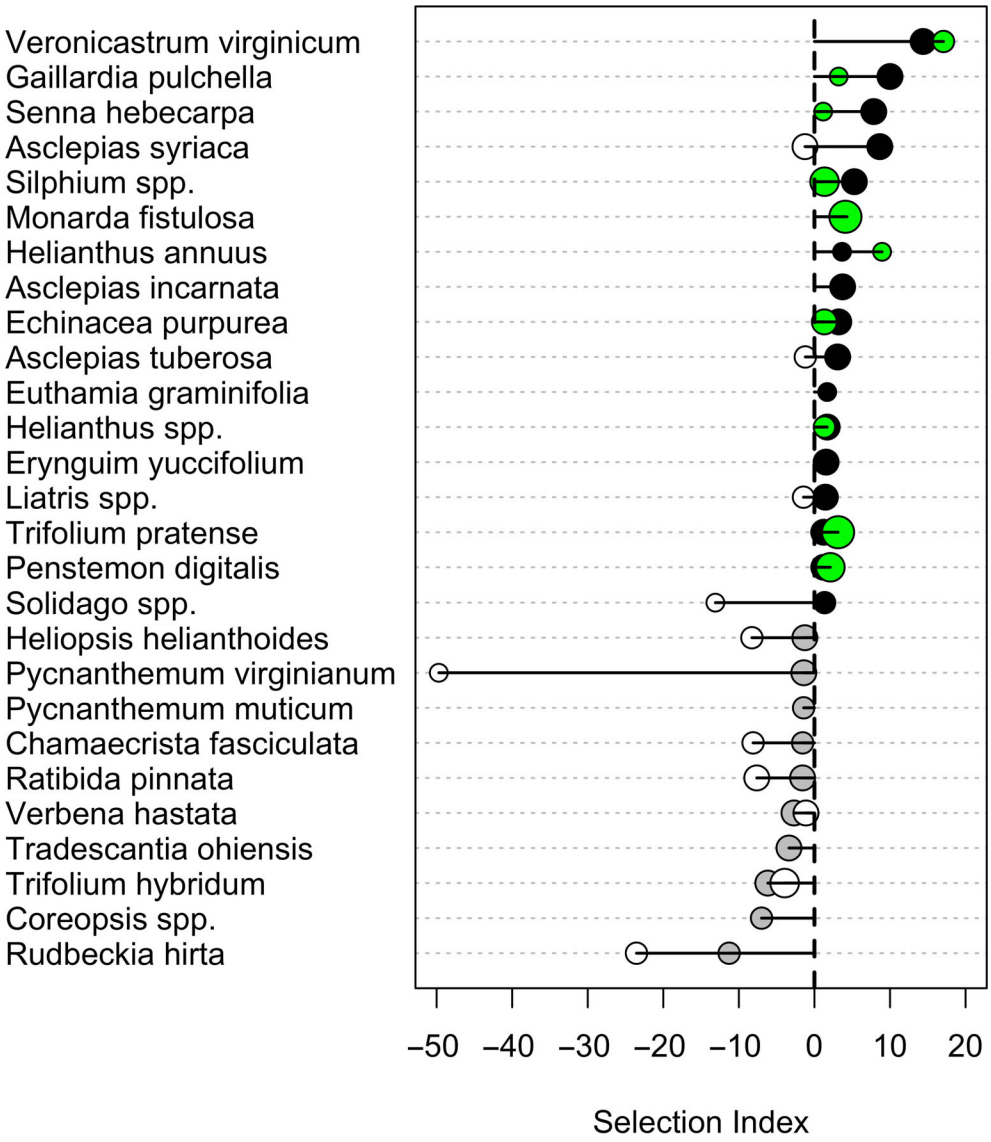



**FIGURE 3** Selection for plant species used in pollinator restoration plantings by common versus rarer bumble bee species. Plant species are listed in order of decreasing aggregated selection ratio index in the three most common *Bombus* species: *B. impatiens*, *B. griseocollis*, and *B. bimaculatus* (black dot if positive selection, gray if negative). Selection by rarer *Bombus* species (*B. vagans*, *B. fervidus*, *B. perplexus*, *B. auricomus*, and *B. pensylvanicus*) is shown as a green dot if positive, white if negative. Dot size is proportional to the number of *Bombus* species that used that plant, with the smallest used by one bee species and the largest by five bee species in that species group.

the highest selection ratios that were used by at least five bee species included a mix of high-quality natives common in regional pollinator habitat restoration, as well as non-natives. For example, in June, bumble bees strongly selected the native plants common in pollinator habitat restorations *Baptisia alba* and *Penstemon digitalis* and the non-native Fabaceae *Lathyrus latifolius*, *Securigera varia*, *Trifolium pratense*, and *Vicia* spp. (Figure 4). In July, the most strongly selected plants that supported at least five *Bombus* species were: *Asclepias* spp., *Calystegia sepium*, *Dipsacus* spp., *Echinacea purpurea*, *Monarda fistulosa*, *Silphium* spp., and *Vicia* spp. Several of these (*Dipsacus*, *Monarda*, and *Silphium*) remained strongly selected in August. In addition, *Helianthus* spp., *Verbena hastata*, and *T. pratense* were also favored (Figure 4). Among plants that supported at least five *Bombus* species, *Trifolium hybridum* and *Melilotus alba* had the lowest negative selection values in both June and July. Note that in August, fewer plant species qualified for inclusion in our assessment of seasonal diet changes (visited by five or more *Bombus* species in any one month), in part because most species except *B. impatiens* were uncommon after the first week of August.

## How do bumble bee species differ in their flower preferences?

For the three most common *Bombus* species, asymptoting rarefaction curves indicated that we were able to detect almost all plant species in their summer diets (Figure 5). However, for five less common species, despite our large sampling effort, the rarefaction curves had not yet plateaued. This result indicates that for diet generalists

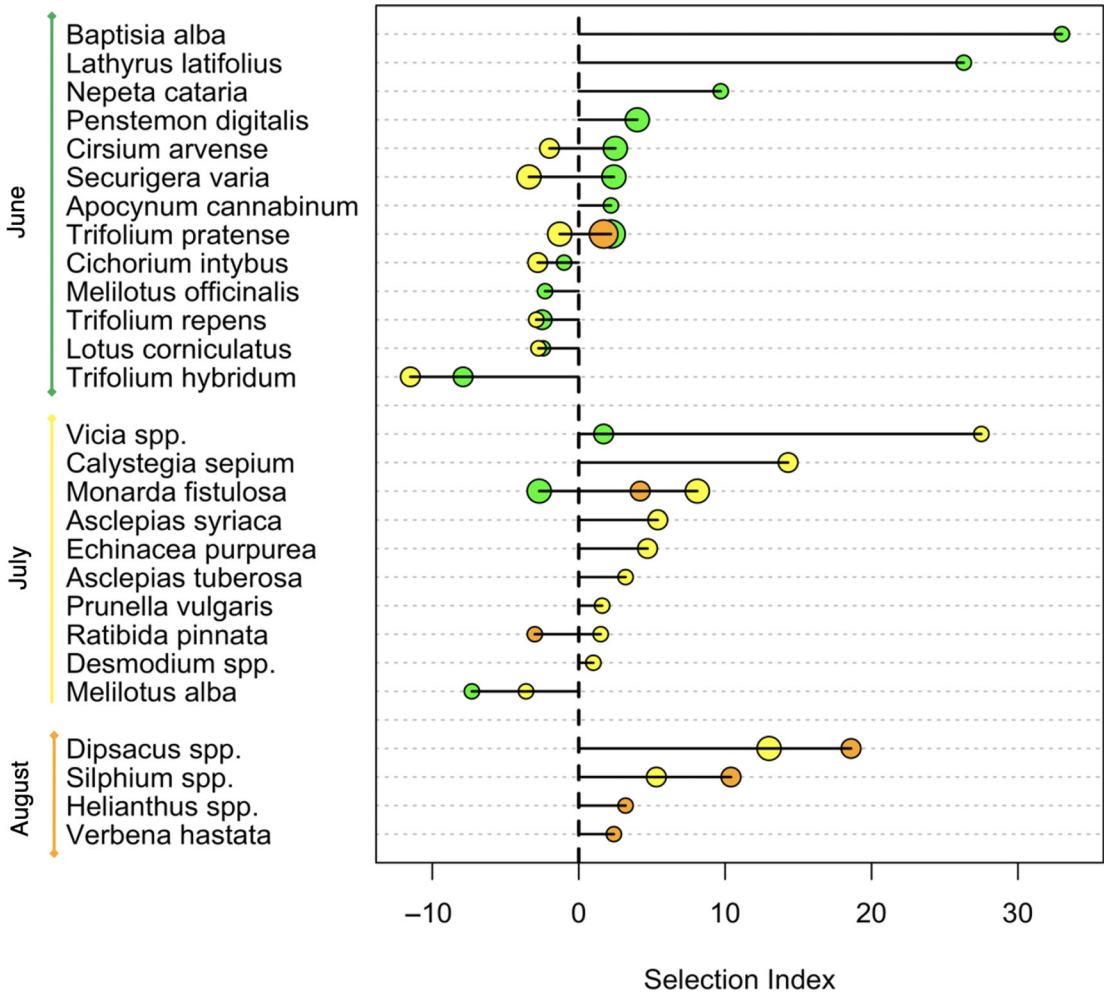



**FIGURE 4** Bumble bee food plant selection by month. Selection was evaluated by selection ratio index, based on data aggregated by month. Only plants that attracted five or more bumble bee species in each month are shown here. Plants are grouped by the month in which they were most strongly selected (although most occurred in multiple months), then in order of decreasing selection index within month. June, July, and August selection indexes are shown by green, yellow, and orange, respectively. Dot size is proportional to species richness of *Bombus* visitors, with the smallest visited by five bee species and the largest by eight species.

like *Bombus* it will take many thousands of observations per species to determine the extent of their flower resource use (Figure 5). Therefore, to evaluate differences in the diets of *Bombus* species, we first considered overall differences in flower use between species while holding bee abundance constant through rarefaction, and then scored *Bombus* species' preferences for certain plants by selection index.

Mean rarefied niche overlap between bumble bee species pairs suggested strong differences in diet (Table 2). For example, the two most abundant species by far—*B. impatiens* and *B. griseocollis*—overlapped in resource use by only about 30% with other species. A follow-up test revealed significant differences in site-level flower use among the three most common species—*B. impatiens*, *B. griseocollis*, and *B. bimaculatus* (adonis PERMANOVA test with post hoc species comparisons; overall $F = 5.691$, $df = 7$, $p = 0.001$). However, diets of the less common species were not well resolved. We were not able to detect significant differences in flower use among three long-tongued species of conservation interest—*Bombus vagans*, *B. fervidus*, and *B. pensylvanicus* (Appendix S1: Table S6). *Bombus pensylvanicus* was similar in flower resource use to *B. auricomus*, another large-bodied grassland species. Another of the rarer species, *B. perplexus*, differed significantly in site-level flower use from all except

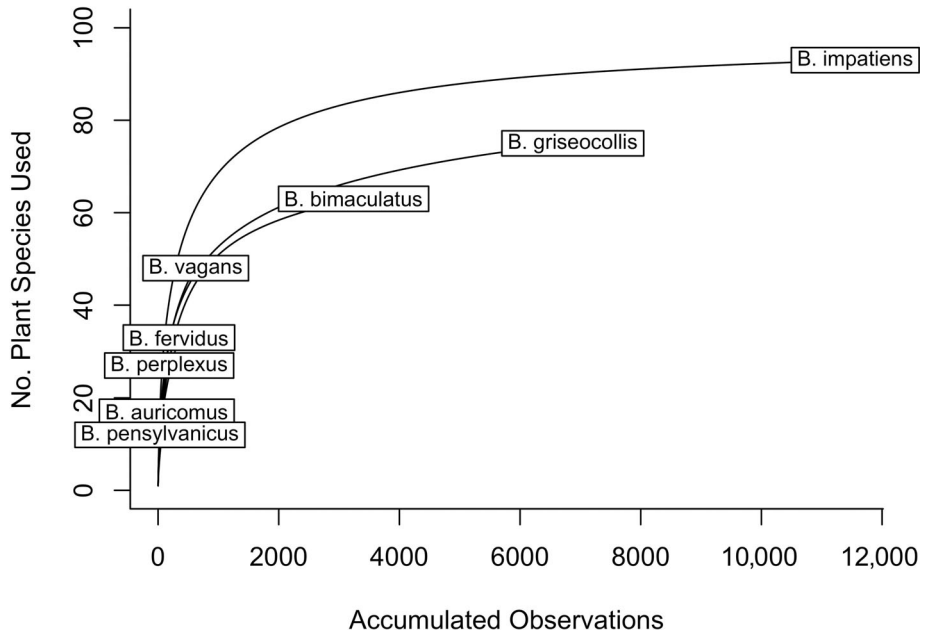



**FIGURE 5** Accumulation of plant species used by *Bombus* with increasing number of individuals observed. Plot generated using rarecurve function in R "vegan" package.

**TABLE 2** Mean rarefied *Bombus* diet niche overlap.

| Species | B. impa | B. gris | B. bima | B. vaga | B. ferv | B. perp | B. auri |
|---|---|---|---|---|---|---|---|
| B. gris | 0.33 ± 0.10 | | | | | | |
| B. bima | 0.37 ± 0.10 | 0.35 ± 0.10 | | | | | |
| B. vaga | 0.36 ± 0.10 | 0.31 ± 0.10 | 0.46 ± 0.11 | | | | |
| B. ferv | 0.32 ± 0.10 | **0.27 ± 0.09** | 0.43 ± 0.12 | **0.55 ± 0.10** | | | |
| B. perp | 0.29 ± 0.10 | **0.28 ± 0.09** | 0.41 ± 0.11 | 0.33 ± 0.10 | **0.28 ± 0.10** | | |
| B. auri | 0.33 ± 0.10 | 0.31 ± 0.10 | **0.51 ± 0.11** | 0.35 ± 0.10 | 0.34 ± 0.10 | **0.23 ± 0.09** | |
| B. pens | 0.38 ± 0.10 | 0.38 ± 0.10 | **0.55 ± 0.09** | 0.44 ± 0.09 | 0.42 ± 0.09 | **0.28 ± 0.09** | **0.60 ± 0.08** |

*Note*: Total visits per species were rarefied to 20 individuals per species 1000 times (rrarefy function, "vegan" package, R). For each randomly resampled community, niche overlap was calculated as the Schoener index (niche.overlap function, "spaa" package, R). Mean niche overlap between species averaged across the 1000 iterations is shown here, along with standard deviation. Species are in order of decreasing total abundance. Species names are abbreviated as B. impa = *B. impatiens*, B. gris = *B. griseocollis*, B. bima = *B. bimaculatus*, B. vaga = *B. vagans*, B. ferv = *B. fervidus*, B. perp = *B. perplexus*, B. auri = *B. auricomus*, B. pens = *B. pensylvanicus*. The three highest and three lowest appear in boldface.

*B. pensylvanicus* (Appendix S1: Table S6) and showed especially low rarefied niche overlap with others (Table 2). Note that species' distribution and frequency in surveys and their annual activity span may have dampened our ability to detect differences in their diets. Both raw and rarefied diet breadths differed substantially among species, from a breadth of only 12 plant species used by *Bombus pensylvanicus* (mean of 9 when rarefied) to a breadth of 93 for *B. impatiens* (13 when rarefied) (Table 3). Both rarefaction curves (Figure 5) and mean rarefied diet breadth (Table 3) suggest that our less abundant species, especially *Bombus vagans* and *B. perplexus*, had broader diets than we observed. A long species activity span tended to be associated with higher rarefied diet breadth, but the trend was not significant ($t = 2.07$, $df = 7$, $p = 0.08$, $r = 0.64$).

Species-level analysis revealed differences in the plants that are strongly selected by common bumble bees, as well as those of conservation interest. Among plants that co-occurred with each of the most common bumble bee species in at least five surveys, *B. impatiens* strongly selected (selection index >10) *Hypericum prolificum*, *Cirsium vulgare*, *Veronicastrum virginicum*, and *Senna hebecarpa*; *B. griseocollis—Asclepias* spp., *Gaillardia pulchella*, *Cirsium vulgare*, *Rosa* spp., and *Dipsacus* spp.; *B. bimaculatus—Convolvulus arvensis*, *Rosa* spp., and *Cirsium vulgare*. Among plants that co-occurred with each of the rarer bee species in at least three surveys, the food plants with selection values >10 for *B. pensylvanicus* were *Asclepias tuberosa* and *Monarda fistulosa*. For *B. perplexus—Dipsacus* spp., *Penstemon digitalis*, and *Silphium* spp. For *B. fervidus—Baptisia* spp., *Dipsacus* spp., *Liatris* spp., and *Eutrochium fistulosum*. And for *B. vagans—Cirsium vulgare*, *Convolvulus arvensis*, *Dipsacus* spp., and *Helianthus* spp.

There were some commonalities in plant selection across bee species (Figure 6). *Dipsacus* spp. scored in the top 5% for four of five of the rarer *Bombus* species. *Cirsium vulgare* was strongly preferred (selection value >10) by all three most abundant bumble bee species and one of the rarer ones (*B. fervidus*), although not always ranking in the top 5%. In addition, *Calystegia sepium*, *Monarda fistulosa*, and *Trifolium pratense* also scored in the top 5% of selection values for three bee species (Figure 6). Consistently least preferred (negatively selected by three or more bee species) were three very common plants (in the top 10% by floral abundance, Appendix S1: Table S1), two of which were used in pollinator conservation plantings: *Trifolium hybridum* and *Rudbeckia hirta*. Several plants were positively selected by some bumble bee species yet avoided by others (Figure 6). However, those cases involved less common bee species, so this pattern may have been an artifact of low sample size, or due to a mismatch in peak activity of the bee and the plant (e.g., *B. auricomus* is most active later in the season when most *Penstemon digitalis* have finished flowering).

Planted meadows are of particular interest for restoration and conservation, so we evaluated bee species' flower preference separately in that habitat. In restored meadows, bees showed strong positive selection for these planted species (among plants that co-occurred with each common bee species in at least five surveys, or three for rarer bee species): *Monarda fistulosa*, *Asclepias syriaca*, *Echinacea purpurea*, *Penstemon digitalis*, and *Silphium* spp. (Appendix S1: Table S7). However, even in these

**TABLE 3** Diet breadth of Ohio bumble bee species.

| Species | Total visits | Activity span in growing degree days (GDD) | Total plant species used | Mean plant species used per 20 bees |
|---|---|---|---|---|
| *B. impatiens* | 11,555 | 1743 | 93 | 12.88 ± 1.76 |
| *B. griseocollis* | 6874 | 1630 | 75 | 11.00 ± 1.78 |
| *B. bimaculatus* | 3241 | 1704 | 63 | 8.22 ± 1.64 |
| *B. vagans* | 624 | 1669 | 48 | 10.19 ± 1.69 |
| *B. fervidus* | 346 | 1448 | 33 | 8.68 ± 1.55 |
| *B. perplexus* | 184 | 1641 | 27 | 10.46 ± 1.66 |
| *B. auricomus* | 144 | 1273 | 17 | 6.01 ± 1.46 |
| *B. pensylvanicus* | 31 | 1137 | 12 | 8.84 ± 1.18 |
| Total | 22,999 | 1795 | 96 | 12.55 ± 1.79 |

*Note*: Species are listed in order of decreasing total abundance. Also given is the activity span of workers of each species in units of GDD, last minus first GDD observed. For the last column, use was rarefied to 20 individuals per species from aggregated total visits and resampled 1000 times without replacement (function rrarefy, "vegan" package in R). The mean rarefied number of plant species used ±SD is given here. The mean rarefied plant species used for total *Bombus* was calculated separately (with 20 random individuals per permutation without respect to species identity).

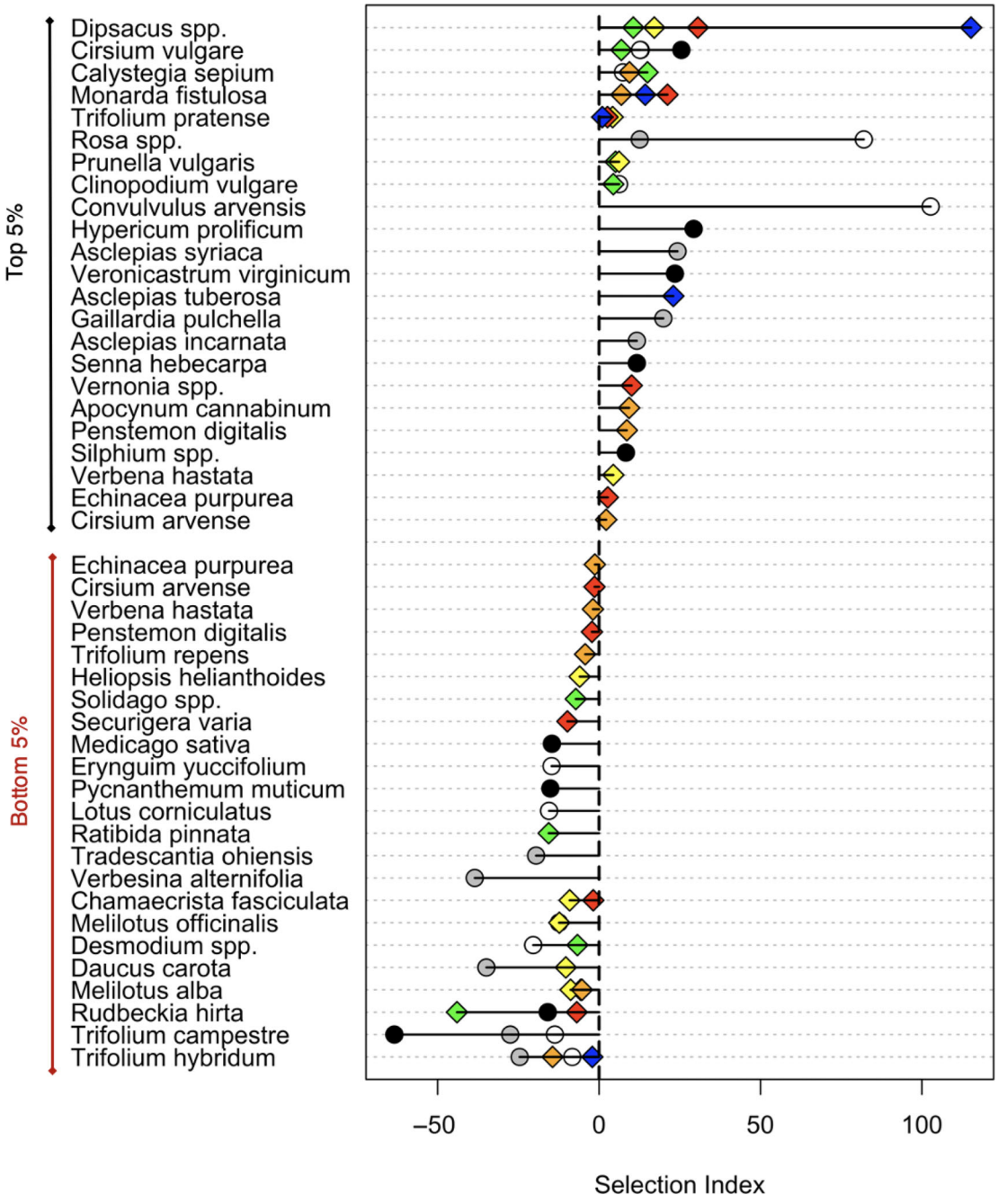



**FIGURE 6** Most strongly selected and avoided food plants by bumble bee species. Floral preference was evaluated by selection ratio based on data aggregated by bee species. Only plants that co-occurred with each bee species in at least five surveys (or three for *B. auricomus* and *B. pensylvanicus*) were considered. Plants shown here scored in the top or bottom 5% of selection index values for at least one *Bombus* species. Plants are listed in order of most to least species that highly selected or avoided that plant, then by decreasing selection. Symbols are color coded by bee species: *B. impatiens* (black), *B. griseocollis* (gray), *B. bimaculatus* (white), *B. vagans* (green), *B. fervidus* (yellow), *B. perplexus* (orange), *B. auricomus* (red), and *B. pensylvanicus* (blue). The three most common bee species are shown as circles and the rarer species as diamonds.

high-quality foraging habitats, some of the most strongly selected plants were "weeds": *Dipsacus* spp., *Cirsium vulgare*, and *Convolvulus arvensis*. In contrast, two species commonly used in pollinator-friendly seed mixes were strongly selected against (*Ratibida pinnata* and *Rudbeckia hirta*). Indeed, although these two were very abundant in planted meadow surveys (>16,000 *Ratibida pinnata* flowering heads and >13,500 *Rudbeckia hirta*), we observed relatively few bumble bee visits to them (602 on *Ratibida pinnata* and 29 on *Rudbeckia hirta*). Seven out of the 10 plant species that were negatively selected in at least three restored

meadow surveys by two or more *Bombus* species were non-native members of the Fabaceae family (*Lotus corniculatus*, *Melilotus alba*, *M. officinalis*, *Securigera varia*, *Trifolium hybridum*, *T. pratense*, and *T. repens*) (Appendix S1: Table S7). Trends in selection and avoidance of plant species commonly used in pollinator plantings were generally similar between common and rarer bumble bee species, although the magnitude of selection differed between the two groups (Figure 3).

## DISCUSSION

Bumble bees are generalist foragers and are active over a long flowering season during which they visit multiple plant species with overlapping phenologies. Resource managers are faced with the challenge of providing high-quality forage for bees across the season but have little data on bee food plant preference with regard to availability on which to base their decisions. Our study of over 22,000 individual bumble bees over a large area of the Midwestern United States evaluated bumble bee plant selection, accounting for both use by bees and floral availability. We quantified preference for and against particular plant species by the genus *Bombus* as a whole, and by individual species, and compared among foraging habitats and across the summer flowering season.

### Which plants are most strongly selected or avoided by bumble bees?

We found strong nonrandom patterns of flower species visitation by *Bombus* foragers, that is, use of some plant species in greater proportion than their abundance would suggest (Cole et al., 2020; Simanonok et al., 2021; Sponsler et al., 2022). Adjusting for flower abundance with the selection ratio index, the plants that Ohio bumble bees most strongly preferred were *Asclepias* spp., *Cirsium* spp., Convolvulaceae, *Dipsacus* spp., *Echinacea purpurea*, *Monarda fistulosa*, *Penstemon digitalis*, *Silphium* spp., and certain Fabaceae. In contrast, other plant taxa were visited much less than expected based on their abundance (e.g., *Trifolium hybridum*, *Melilotus* spp.). Several taxa that were abundant in more than 10% of surveys had fewer than five bumble bee visits (*Achillea*, *Erigeron*, *Leucanthemum*, *Medicago*, and *Oxalis*). It is hard to draw conclusions about negatively selected plants in our dataset using the selection index because it is undefined (but presumed negative) for 40 plant taxa that were present in flower abundance surveys but received zero bumble bee visits. Likewise, the index is undefined (but presumed positive) for 36 plant taxa that were visited by *Bombus* during bee surveys but not captured by the corresponding flower transect surveys. These limitations reflect imprecise abundance and visitation estimates for uncommon plant species.

Managers seeking to enhance foraging habitat for bumble bees should not only include highly used flowers, but also highly preferred flowers, and the selection index provides the latter information more precisely than does raw use. Indeed, our assessments of bee food plant choice changed dramatically when we accounted for floral availability. For example, the top plant species based on use was *Monarda fistulosa* (20.8% of all *Bombus* visits). However, it dropped to 16th most selected when availability was accounted for (4.8% of all surveyed floral units). *Cirsium vulgare* ranked 36th based on raw use (0.37% of *Bombus* visits) but rose to no. 1 in the selection index because this small number of visits was observed on a much smaller number of available flowers (0.02% of all floral units). Choosing to include species in plantings that have high selection indices but low natural abundances (like a *Cirsium* sp., *Hypericum prolificum*, or *Veronicastrum virginicum*) might be especially productive. However, as a rule of thumb, selection index values for plant species that make up less than 0.1% of the available flowering units should be treated with caution because estimates of abundance for uncommon species are likely less precise and more variable. Low abundance may help explain the unexpectedly high selection ratios we found for *Calystegia* and *Convolvulus*. Limiting attention to plants with over 0.1% total abundance, the highest selection indices were for *Dipsacus* spp., *Asclepias syriaca*, *Silphium* spp., *Monarda fistulosa*, and *Echinacea purpurea*.

Likewise, limitations of the selection ratio index suggest caution for interpreting results for highly abundant plant species, such as some in the Fabaceae that are often included in restoration plantings and are recognized as highly desirable forage for *Bombus* (Gibson et al., 2019; Goulson et al., 2005; Wood et al., 2019, 2021). For example, negatively selected species such as *Securigera varia*, *Trifolium repens*, and *Lotus corniculatus* were highly used by bumble bees at least during their peak bloom, yet their extreme abundance contributed to low selection ratios. If these abundant resources saturated the local bumble bee community or interfered with the ability to accurately survey visitors, then the selection ratio index would underestimate their value. On the other hand, some negatively selected Fabaceae that were highly abundant were not among the most highly visited species, including *Melilotus* spp. and *T. hybridum*. We note with surprise that in our study only a few Fabaceae (*Baptisia* spp., *Trifolium pratense*, and *Vicia* spp.) were highly selected. Although

this family includes valuable forage species for *Bombus* in the Midwestern US habitats that we sampled, some species of Fabaceae clearly were less useful for bumble bees than others and therefore make poor choices for bumble bee habitat restoration.

Two other factors that may have led us to over- or underestimate the importance of some plant taxa for bumble bees are that we did not distinguish (1) male versus female visits or (2) pollen versus nectar visits when calculating preference. By combining castes, we may have underestimated the preference for plant taxa used exclusively for pollen, which would not receive visits from males. In contrast, if a plant was primarily visited by the males of a species, it would not greatly contribute to colony growth or gyne production. In our dataset, however, plants that ranked as most preferred in the aggregate dataset were visited by both males and workers. In a subset of our data for which we distinguished caste, among the most highly selected food plants of the most common *Bombus* species, there were no instances where males used a plant taxon that workers did not (Appendix S1: Table S8). And there was only one instance in one bee species where more males than workers were observed on a plant taxon (*B. griseocollis* visits to *Silphium* spp.). It is also important to note that by not distinguishing pollen from nectar visits, we may have overestimated the importance of plants that were used for nectar only (like milkweeds, *Asclepias* spp.). In contrast, we may have underestimated the importance of plants that did not rank highly by the overall selection index but are key pollen resources for colony growth. For example, *Trifolium pratense* was not in the top 10% of preferred food plants for most bee species but is known to be an important pollen source, especially for the long-tongued species *B. auricomus*, *B. pensylvanicus*, *B. fervidus*, and *B. vagans* (Wood et al., 2019).

## How does bumble bee floral use and selection differ among habitats, particularly in managed pollinator habitat compared with unmanaged habitats?

Restored pollinator meadows are a habitat of particular interest for bee conservation. We found bee diets in that habitat strongly differed from diets in other habitats, despite some overlap in flower composition (Appendix S1: Table S3). This observation dovetails well with evidence that individual bumble bees make context-dependent foraging choices (Bruninga-Socolar et al., 2022; Heinrich, 1979). The plants that contributed the most to differences in diets between restored pollinator meadows versus other habitats generally overlap with our preferred list above (highly influential taxa in *Bombus* diets that were more common in planted meadows: *Asclepias*, *Echinacea*, *Monarda*, and *Penstemon*; more common in other habitats: *Dipsacus*, *Securigera*, and *T. pratense*). The low selection index score of *Rudbeckia hirta* is a notable exception, suggesting that this species may not provide much benefit to *Bombus* in restoration plantings. When restricting attention to plants used in pollinator habitat restoration (Figure 3), we noted plants that were strongly selected in planted meadows but that were not listed as preferred plants in Table 1 because they were used by fewer than five *Bombus* species: *Veronicastrum virginicum*, *Gaillardia*, and *Senna hebecarpa*. These plants were strongly selected by a few of the more common bumble bees (*B. impatiens* and *B. griseocollis*; Appendix S1: Table S7), suggesting that they could be helpful for supporting common species of *Bombus* in the Midwestern United States and in situations when promoting rare species are not the main focus.

## How does bumble bee flower selection vary across the growing season?

High-quality bumble bee habitat offers floral resources throughout their long flight period from queen emergence to colony senescence (Colla, 2016). During the months of peak bumble bee activity in Ohio (June–August), plant selection varied widely (Figure 4), in part related to changes in plant phenology. June's list of food plants that support diverse *Bombus* was dominated by *Baptisia alba* and *Lathyrus latifolia* (Fabaceae). July and August's top food plants were high-quality pollinator restoration species (*Asclepias* spp., *Monarda fistulosa*, *Echinacea purpurea*, *Silphium* spp., and others), in addition to some weeds (most notably *Dipsacus* spp.). A few species with long bloom times were highly selected in multiple months, but most plant species were positively selected in only one month.

Managers designing planting schemes may find it useful to include a seasonal succession of highly favored plants for the target bee species. For example, a "relay" of native species might include *Baptisia* (strong selection ratios in June; Figure 3), *Vicia* (strong in July), and *Silphium* (strong in August). Note that in the Midwestern United States, by mid-August most *Bombus* species except *B. impatiens* are much less abundant, so flowers that begin blooming at this time of year would not contribute much to *Bombus* diversity (Novotny et al., 2021). However, they may support gyne production in late-nesting species like *B. pensylvanicus*, which is currently in decline (Hatfield et al., 2015).

Our study is temporally limited both seasonally and by the time of day. Seasonally, we only have data for June–August, the peak season for the bumble bee worker caste in our study region. Therefore, we cannot evaluate the selection for spring or fall flowers, which are essential for queens to establish spring nests and build autumn fat reserves for overwintering (Lanterman et al., 2019; Malfi et al., 2019). Additionally, our study only captured bumble bee choice for plant species visited during the period of 10:00–16:00, eliminating observations of visits to species that specialize in attracting pollinators outside these hours. For example, *Mimulus ringens* (Christopher et al., 2021) and *Tradescantia ohiensis* (Parrish & Bazzaz, 1979) receive most visits before 10:00, while *Oenothera* opens late in the day (Steckel et al., 2019). Therefore, a strong knowledge of the natural history of individual plant species should inform planting decisions.

## How do bumble bee species differ in their flower preferences?

The common *Bombus* species in our survey differ significantly in their feeding niches, which is likely to reduce potential competition for resources among them. Mean niche overlap between species pairs was low, with only a few sharing more than 50% of floral resources, even when abundance per bee species was held constant through rarefaction. This food niche separation suggests a mechanism for co-existence of many otherwise similar species (Heinrich, 1976; Shibata & Kudo, 2020; Sponsler et al., 2022). Differences in species' phenology may also impact resource sharing—*Bombus impatiens*' diet may overlap less with other species because its worker populations peak in August, later than most other species (Novotny et al., 2021).

In contrast, we found high rarefied niche overlap between three of the rarer species that have been elsewhere reported to be in decline—*B. vagans*, *B. fervidus*, and *B. pensylvanicus* (Bartomeus et al., 2013; Cameron et al., 2011; Colla et al., 2012; Grixti et al., 2009; Jacobson et al., 2018; Williams et al., 2009). All three showed strong positive selection index values for *Calystegia sepium* and *Dipsacus* spp., and over 40% of individuals in these bee species were recorded on either *Trifolium pratense* or *Monarda fistulosa*. When we considered which plants were preferred by our long-tongued bumble bees as a group (*B. auricomus*, *B. fervidus*, and *B. pensylvanicus*), the list was the same, but with the addition of *Vicia* spp. One might prioritize floral species that provide forage for these bee species across the months when they are most active, by planting *Trifolium pratense* (June) and *Monarda fistulosa* (July), or by not actively removing *Dipsacus* spp. We advocate a cautious interpretation of the diet data for these bee species, however, because the plant species accumulation curves suggested that our dataset underestimated diet breadth.

Preference for non-native plant species by bumble bees, especially by rare bumble bee species, presents an ecological and conservation conundrum that must be addressed on a case-by-case basis (Gibson et al., 2019) and adds to the complexity of habitat restoration for land managers (Ewel & Putz, 2004). For example, one non-native plant taxa in particular (*Dipsacus*) is considered invasive in Ohio (https://agri.ohio.gov/divisions/plant-health/invasive-pests/invasive-plants), yet it was the most strongly preferred plant by three of our uncommon bumble bee species (*B. auricomus*, *B. fervidus*, and *B. pensylvanicus*). Indeed, for half of our *Bombus* species (*B. auricomus*, *B. bimaculatus*, *B. fervidus*, and *B. pensylvanicus*), the most strongly selected plant species was non-native. Selection indices that account for flower abundance offer guidance on the kind of plants and floral traits selected by bee species of interest, allowing managers to seek similar native or non-invasive congeners as they target resources for particular bumble bees (Colla, 2016; Sponsler et al., 2022). For example, bumble bee preference for the non-native *Cirsium vulgare* could be supplied instead by including the native *Cirsium discolor* in pollinator habitat enhancements.

An important strength of our analysis is that we used rarefaction to more equitably evaluate diet breadth for individual species by accounting for sampling intensity (Gotelli & Colwell, 2001). However, this measure only partially accounts for lack of equivalence in sampling for rare and common bees because rare species were sampled at fewer locations and times, meaning fewer flower species to sample from. For example, randomly sampling 20 individuals of a common species like *B. impatiens* might mean drawing from 20 different sites across different times of the season, while drawing 20 bees for rarer species might mean sampling from only the few places they occurred, on a handful of days, and consequently from a more limited floral community. Perhaps as a result of this shortcoming, we found some unexpectedly large selection ratios. It is sobering to note that despite recording over 22,000 bee–flower associations for a modest bee community of eight species, sample size may be inadequate to fully characterize the diet breadth of more than half of the *Bombus* species in our area.

Our large dataset provides key information about floral preferences of bee populations in the Midwestern United States, but many of these bee species occur over much broader areas of North America. Differences in the floral communities across their ranges likely result in different preferences or rankings of flowers. While these

results may not be directly applicable outside of our region, they could provide guidance in choosing plants of related taxa that occur in other areas. Of course, this approach does not substitute for gathering preference data such as has been done for some regions (Cole et al., 2020). We recommend that researchers incorporate a measure of floral abundance as part of bee surveys to build the datasets needed for evaluating preference. This practice would facilitate comparisons of preference within and across species over a wider geographic region.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Bumble bee floral use and floral abundance data, as well as novel statistical code, are available from Open Science Framework (Novotny, 2022): https://osf.io/ygd9m/?view_only=5f38e8ba1e184b1d8708f32df9a19825.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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