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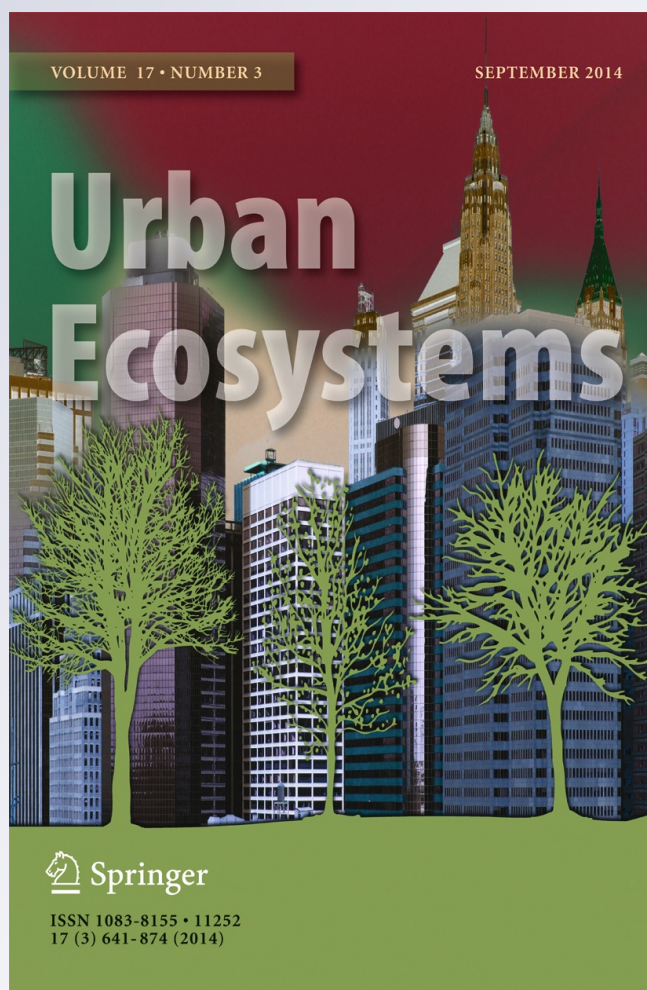
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Native plants are the bee's knees: local and landscape predictors of bee richness and abundance in backyard gardens

Gabriella L. Pardee · Stacy M. Philpott

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Abstract Urban gardens may support bees by providing resources in otherwise resource-poor environments. However, it is unclear whether urban, backyard gardens with native plants will support more bees than gardens without native plants. We examined backyard gardens in northwestern Ohio to ask: 1) Does bee diversity, abundance, and community composition differ in backyard gardens with and without native plants? 2) What characteristics of backyard gardens and land cover in the surrounding landscape correlate with changes in the bee community? 3) Do bees in backyard gardens respond more strongly to local or landscape factors? We sampled bees with pan trapping, netting, and direct observation. We examined vegetation characteristics and land cover in 500 m, 1 km, and 2 km buffers surrounding each garden. Abundance of all bees, native bees, and cavity-nesting bees (but not ground-nesting bees) was greater in native plant gardens but only richness of cavity-nesting bees differed in gardens with and without native plants. Bee community composition differed in gardens with and without native plants. Overall, bee richness and abundance were positively correlated with local characteristics of backyard gardens, such as increased floral abundance, taller vegetation, more cover by woody plants, less cover by grass, and larger vegetable gardens. Differences in the amount of forest, open space, and wetlands surrounding gardens influenced abundance of cavity- and ground-nesting bees, but at different spatial scales. Thus, presence of native plants, and local and landscape characteristics might play important roles in maintaining bee diversity within urban areas.

Keywords Native bees · Urban gardens · Hymenoptera · Pollination · Urbanization

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Introduction

Habitat degradation and fragmentation associated with urbanization can severely impact species richness and composition of animal communities. Areas that are highly urbanized tend to have the lowest biodiversity along an urban to rural gradient, and in urban areas, species diversity of plants, mammals, reptiles, and amphibians decline due to increased fragmentation, increased population isolation, and decreases in habitat connectivity (Dickman 1987; Fahrig 2003; McKinney 2008).

Although there is growing interest in urban biodiversity conservation, and urban landscapes continue to expand globally (UNFPA 2007), we know relatively little about the impact of urbanization on insects, despite their important contributions to ecosystem services. Studying the impacts of urbanization on insect diversity is important for several reasons. First, both insects and other arthropods frequently inhabit disturbed and man-made environments and therefore may be good indicators of how urbanization affects animal communities (Frankie and Ehler 1978). Because arthropods are abundant in the environment and have relatively short generation times, their life histories may allow them to respond rapidly to urbanization, serving as sensitive bioindicators (McIntyre et al. 2001). Insects contribute ecosystem services worth an estimated \$56 billion (USD) in the US alone (Daily 1997; Losey and Vaughan 2006; McIntyre et al. 2001). One of the most valuable ecosystem services provided by insects is pollination, and bees, in particular, pollinate more than 66 % of the world's 1,500 crop species (Kremen et al. 2004). Yet pollination services may decline as bee abundance and richness decline (e.g. Klein et al. 2003). Recent reports on the decline of pollinators have been linked to loss of habitat due to increasing urbanization, agricultural intensification, and fragmentation (Ahm e et al. 2009; Potts et al. 2010). The degradation of natural areas can reduce or eliminate floral and nesting resources pollinators need in order to survive (Potts et al. 2010).

Although urban areas are generally species-poor (Czech et al. 2007), some urban habitats, such as gardens or forest fragments may be suitable for supporting biodiversity (Hernandez et al. 2009; Goddard et al. 2010; Matteson et al. 2012). Urban areas with large amounts of vegetation cover provide habitat for biodiversity (Angold et al. 2006; Savard et al. 2000; Smith et al. 2005). For example, community gardens throughout New York City attract a wide variety of bee species, including many native cavity-nesting bees (Fetridge et al. 2008; Matteson et al. 2008). Urban parks in San Francisco attract more bees and more bee species than larger parks outside the city, suggesting that urban areas can provide important food and nesting resources (McFrederick and LeBuhn 2006). Furthermore, the local features of urban habitats such as floral abundance, garden size, and plant species richness can influence suitability for bee habitation (Frankie et al. 2005), as bee species richness correlates with plant and floral resources in urban areas (Frankie et al. 2005; Matteson and Langellotto 2010). Inclusion of native plants in backyard gardens may attract native bees, but little empirical data demonstrate whether or not native plant presence affects diversity of urban arthropods. Native plants are naturally occurring species that evolved with or migrated naturally to a particular area and were not directly or indirectly introduced through human involvement (Richards et al. 1998). Thus, although fragmentation and urbanization generally are associated with lower bee diversity, incorporating additional resources, such as native plants, into urban green spaces may help promote biodiversity, specifically for pollinators.

In addition to local habitat features, the location of urban habitats (e.g., proximity to large parks) or the landscape surrounding urban habitats may strongly affect bee communities. For example, within New York City, Matteson and Langellotto (2010) found that tall buildings within a 200–500 m radius limited sunlight availability within an urban garden, which could negatively impact bees by limiting plant growth and preventing bees from increasing their

body temperature through passive basking in gardens (Matteson and Langellotto 2010). In contrast, ample urban parks, fragmented forests, wetlands, and community gardens within a 500 m - 1 km radius of a garden may provide corridors and more vegetated landscapes for arthropods and support higher richness (Rudd et al. 2002).

Finally, bees vary in a suite of ecological traits, including body size, degree of sociality, and nesting strategy, which might cause specific bee guilds to respond differently to local and landscape characteristics of urban habitats (Williams et al. 2010). Cavity-nesting bees are favored in urban areas because they can nest in fences and gardens whereas ground nesting bees cannot locate nests in developed areas due to the lack of soil availability (Cane et al. 2006; Matteson et al. 2008; Ahn e et al. 2009; Neame et al. 2013). Foraging distance is positively correlated with body size (Gathmann and Tschardtke 2002) so larger bees might be able to forage farther away from urbanized areas and access a greater number of floral resources, thus having a greater advantage over smaller bees.

In this study, we examined the impact of garden characteristics and the surrounding landscape on bee diversity in urban, backyard gardens of northwestern Ohio. We carried out surveys in backyards containing both flowers and vegetable gardens, and specifically, we examined whether presence of native plants in backyard gardens was associated with changes between the bee communities encountered in the gardens. We examined several characteristics of each backyard garden including size of vegetable and flower gardens, number of flowers, and floral diversity, and performed a landscape analysis to examine land cover types surrounding each backyard. We then investigated three main research questions: 1) Does bee diversity, abundance, and community composition differ in backyard gardens with and without native plants? 2) What specific characteristics of backyard gardens and land cover in the surrounding landscape correlate with changes in bee abundance and richness overall, and for specific groups of bees? 3) Do bees in urban areas respond more strongly to local or landscape factors?

Materials and methods

Study sites

We selected 16 backyard gardens in northwest Ohio in which to collect bees (Fig. 1, Table 1). All gardens were in low-density residential suburbs, except for two cases where the vegetable gardens were located in suburban botanical gardens. Each backyard garden contained vegetable and flower gardens. Eight of the gardens selected had 0 % native plant cover and the other eight gardens had >48 % native plant cover. We first selected gardens with native plants, and then selected a nearby, paired site such that each pair contained one backyard with vegetables and native plants and one backyard with vegetables and no native plants. Paired backyards were located within 0.4 - 8 km of each other. We paired backyards because we wanted to find native and non-native gardens with similar landscape characteristics. In some cases, sites were 8 km apart because we could not locate closer non-native plant gardens to pair with native plant gardens. Backyards differed in the area and arrangement of plantings of vegetables, flowers, and native plants; vegetable plots ranged from 1.44 to 288 m² per backyard, area planted with native flowers ranged from 0 to 450.95 m², and area planted with non-native flowers ranged from 0 to 101.69 m² (Table 1). All vegetable gardens contained similar bee pollinated crops such as tomatoes, squash, beans, cucumbers, peppers, and eggplants and herbs such as basil and sage. Many native gardens contained plants native to Northwest Ohio, including butterfly milkweed (*Asclepias tuberosa*), columbine (*Aquilegia*

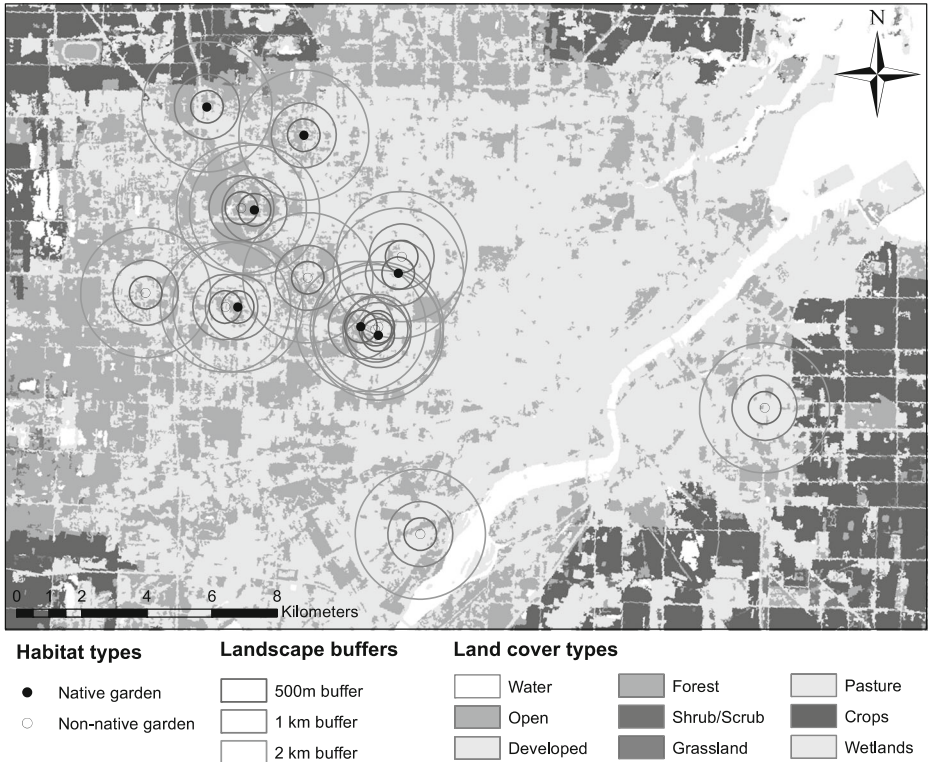


Fig. 1 Map of the study sites in northwestern Ohio

spp.), asters (*Aster* spp.), coneflowers (*Echinacea* spp.), and brown-eyed Susans (*Rudbeckia* spp.). Most gardens also contained flowers not native to the region, including marigolds (*Tagetes* sp.), sunflowers (*Helianthus annuus*), roses (*Rosa* spp.), lilies (*Lilium* spp.), and zinnias (*Zinnia* spp.) (see Table S1 for a list of the most common plant species encountered).

Bee sampling

To assess our first question, we used three methods to collect and observe bees between May and August, 2010: hand-netting, pan trapping, and direct observation. We chose to use both pan trapping and hand-netting in order to adequately measure the diversity of bees within each garden and we used direct observations to study which bees were visiting the flowers and crop species. Bees were netted by hand once a month in each site in June, July, and August. In order to examine which bees were visiting the native and non-native plants and to better measure the bee community present within each backyard, we netted for 30 min within a 2×2 m plot in the native or non-native garden nearest to the vegetable gardens at each site (between 4 and 6 m away). To capture temporal variation in foraging activity of different species, we netted at each site both in the morning (9–12 AM) and again in the afternoon (1–4 PM) on the same day.

We collected bees using pan traps in May and July. For pan trapping, we used three 355 ml bowls (one yellow, blue, and white, 15 cm diameter, 4.5 cm depth, Solo brand) per site filled with a solution consisting of 300 ml of water and 4 ml of detergent to act as a surfactant (Dawn, Cincinnati, OH). We placed the pan traps in the vegetable gardens in a triangular

Table 1 Descriptive data of backyard gardens in northwestern Ohio

| Garden number | Garden pair | Garden type | Native flower area (m ²) | Non-native flower area (m ²) | Vegetable area (m ²) |
|---------------|-------------|-------------|--------------------------------------|--|----------------------------------|
| 1 | 9 | Native | 171.95 | 0 | 3.75 |
| 2 | 15 | Native | 36 | 0 | 4.8 |
| 3 | 10 | Native | 12.71 | 2.42 | 55.73 |
| 4 | 16 | Native | 172.58 | 0 | 9.57 |
| 5 | 13 | Native | 7.47 | 8 | 8.6 |
| 6 | 11 | Native | 11.58 | 5.82 | 18.35 |
| 7 | 12 | Native | 450.95 | 0 | 7.05 |
| 8 | 14 | Native | 86.9 | 12 | 1.44 |
| 9 | 1 | Non-native | 0 | 110 | 5.06 |
| 10 | 3 | Non-native | 0 | 16.59 | 6.68 |
| 11 | 6 | Non-native | 0 | 88.16 | 28.76 |
| 12 | 7 | Non-native | 0 | 86.02 | 133.75 |
| 13 | 5 | Non-native | 0 | 29.28 | 30.21 |
| 14 | 8 | Non-native | 0 | 21.1 | 10 |
| 15 | 2 | Non-native | 0 | 101.69 | 288 |
| 16 | 4 | Non-native | 0 | 37.1 | 6.88 |

pattern with 5 m between traps. We elevated traps 1 m above ground by placing them on a PVC pipe with a metal wire looped around the top of the pipe to hold the bowl in place. Bowls were set out between 8 and 9 AM and collected between 2 and 3 PM. At collection, we poured the trap contents into a mesh strainer, and washed insects with water and rinsed them with 70 % ethanol (LeBuhn et al. 2003; Matteson et al. 2008). Within 24 h of collection, we dried insects with paper towels and pinned them for later identification.

We conducted direct observations at each site once a month from May - August between 9 AM and 2 PM on calm, sunny days (Tuell et al. 2008). We randomly selected a 2×2 m plot within each vegetable garden and observed bees for 15 min, noting both the number of bee individuals and the identity of each bee that landed within the plot. We grouped bees as honeybees, bumble bees, or other bees. We chose those three groups as they were the easiest to identify in the field. We included all bee observations where the bee landed on any vegetation or plant part (flower, fruit, leaf, etc.) within the 2×2 m plot. We recorded the plant species where bees landed and the color of the flowers, if any, on that plant. We did not specifically assess the number of flowers visited by each bee individual. We repeated the 15 min observation in another 2×2 m plot within the vegetable garden to make a total observation time of 30 min. In backyards with multiple vegetable beds, we rotated the observation plot location between beds and selected the plot at random within individual beds. Bumble bees and others were collected for later identification. All specimens are currently housed at the U. of California, Santa Cruz.

Vegetation and floral measurements

To test our second hypothesis, we sampled several vegetation characteristics to assess correlations between vegetation and abundance and richness of bees. Within 3 days after pan trapping was conducted, we sampled vegetation in each of the gardens. We used a convex

spherical densiometer to measure the amount of canopy cover directly over the vegetable garden and 5 m away from the garden in each cardinal direction. We estimated the number of flowers within a 25 m radius of the pan traps. Where flowers were highly abundant (>100 flowers), we recorded an approximate number of flowers within the 25 m area by counting all flowers in a smaller area (few square meters), and extrapolating from that the floral abundance of a given species in the entire 25 m area. We sampled ground vegetation within the two 2 × 2 m bee observation plots in each site, on each observation date. For each plot, we recorded the number of all plant species (both flowering and non-flowering) and identified each to morphospecies. We also recorded the height of the tallest vegetation and the percent cover provided by herbaceous species, woody species, grass, hay, stones/bricks, mulch, and bare ground. We defined mulched areas as those areas that were intentionally covered with a thin layer of leaves, bark, or compost by the property owners. Within the 2 × 2 m plots, we recorded floral abundance by counting the total number of flowers, and noting the color of each flowering plant. As a rough estimate of floral volume per plot, we measured the corolla width and length of one haphazardly selected flower per species. We then estimated floral volume by multiplying the volume of an individual flower by the total number of flowers of that species, and then summing across species.

Land cover types in the surrounding landscape

To address our third hypothesis, we used a geographic information system (GIS) to examine the land cover types surrounding each study site. We obtained land cover data for Lucas County, OH, from the 2001 National Land Cover Database (NLCD, 30 m resolution) (Homer et al. 2004), and used these data to calculate the percentage of different land cover types in buffers surrounding each backyard site. We grouped the land cover types encountered and described by Homer et al. (2004) into seven categories: 1) open water, 2) wetlands (including woody and emergent herbaceous wetlands), 3) open space (usually including lawn grass, parks, golf courses, vegetation in developed areas), 4) developed areas (including low, medium, and high intensity), 5) forest (including deciduous and evergreen forest), 6) grassland/herbaceous, and 7) agriculture (including cultivated crops and pasture/hay fields). We assessed the percentage of each land cover type in 500 m, 1 km, and 2 km buffers around each site as they correspond to typical bee flight ranges (Brown and Albrecht 2001; Gathmann and Tschamtkke 2002; Heard et al. 2007).

Statistical analyses

We examined whether presence of native plants affected abundance and species richness of bees. We examined patterns for netting and pan trapping (the two methods that captured the most bees) alone, and also compiled all data for netting, pan trapping, and observations across all sites to compare abundance and richness between gardens with and without native plants. We compared the mean number of individuals and species collected per site (for all bees, native bees, cavity-nesting bees, and ground-nesting bees) in native vs. non-native gardens with linear mixed models with the lme function in the 'nlme' package in R (Pinheiro et al. 2013; R Development Core Team 2011). We included garden type (native or non-native) as a fixed factor, and included site (pair number) as a random factor. As the question was to examine differences in garden types, we included garden type as a fixed factor, and used the restricted maximum likelihood or 'reml' method.

We created species accumulation curves for bees collected with netting, pan trapping, and all methods in native and non-native gardens for observed richness (Mao Tao) with EstimateS

v. 8.2 (Colwell 2009). Species accumulation curves helped us determine how well we sampled at each site. When the species accumulation curves reach an asymptote, then the sampling effort has been sufficient in collecting most of the species present at each site. We created species sample curves rescaled to the number of individuals, and compared observed and estimated richness in the different garden types with 95 % confidence intervals (CI).

We examined differences in bee community composition in the native and non-native gardens in three ways. First, we used non-metric multidimensional scaling (NMDS) to visually compare species similarity of the sampled sites. We used PAST (Hämmer et al. 2001) to create NMDS plots with the Bray-Curtis similarity index, and only included in the analysis those bee species collected from more than one individual. We tested the significance of visually distinguishable groups resulting from NMDS solutions using a 1-way analysis of similarities (ANOSIM), a nonparametric significance test based on the Bray-Curtis similarity index (Arscott et al. 2006). ANOSIM calculates mean distance within a habitat type and between sites of different habitat type to determine if sites of an individual habitat type are clustered. The global p-value then denotes significant differences of between and within habitat similarity (Philpott 2010). Finally, we conducted a NPMANOVA with the Bray-Curtis similarity index to determine if sites of one habitat type or the other were more closely clustered. We also visually examined the clustering of common species (those collected from more than 10 individuals) in native or non-native gardens by plotting their distributions on NMDS plot.

To determine the importance of vegetation factors (local) and the land cover types (landscape) in the surrounding landscape for bee abundance and richness, we used conditional inference trees (Hothorn et al. 2006). We constructed conditional inference trees with the 'party' package in R. Classification and conditional inference trees examine the degree to which certain factors predict a dependent variable, and determine the relative importance of individual factors (Olden et al. 2008; Strobl et al. 2009). Specifically, conditional inference trees utilize a binary recursive data-partitioning algorithm to estimate relationships between suites of predictor variables (Hothorn et al. 2006). The iterative process includes examining each variable to search for the best predictor, splitting the data for the dependent variable into two distinct groups, and then repeating the variable selection until no more significant predictors are found. For the analysis we included 17 predictor variables that were recorded within each backyard and an additional 19 variables pertaining to the surrounding landscape to examine the importance of both local and landscape factors for bee abundance and richness (Table 2). No grassland, herbaceous area, or agriculture was found within 500 m of the study sites. Our 18 response variables were numbers of bee individuals and species in pan traps, observation, and netting, and the numbers of cavity-nesting and ground-nesting individuals and species in pan traps, observation, and netting. We used raw, untransformed values for all predictor variables, and log transformed (LN+1) values for the response variables.

To examine whether the proximity of sample plots influenced the conditional inference tree results, we tested for spatial autocorrelation in the dependent variables (Dormann et al. 2007). We examined the degree of spatial autocorrelation in the residuals of the conditional inference trees with (1) spatial correlograms (R package 'nct') and (2) the Moran's test for spatial autocorrelation using a spatial weights matrix. For correlograms, we computed 100 permutations using the 'resamp' argument in the correlog function to examine the distance, if any, at which variables were spatially autocorrelated. For the calculation of Moran's I, we used nearest neighbor distances as the metric, and used the permutation test option. None of the dependent variables displayed any spatial autocorrelation (Table S2).

Table 2 A list of the local and landscape factors included as predictors of bee abundance and richness in the conditional tree analyses and the range of values measured for each factor

| Factor scale | Scale at which measured | Factors | Range of values measured |
|--------------|-------------------------|-----------------------------------|----------------------------|
| Local | 2 m×2 m plot | No. of plant species | 2.5–20.5 |
| Local | 2 m×2 m plot | Woody species cover (%) | 0–90 % |
| Local | 2 m×2 m plot | Herbaceous plant cover (%) | 7.5–95 % |
| Local | 2 m×2 m plot | Bare ground cover (%) | 0–77.5 % |
| Local | 2 m×2 m plot | Mulch cover (%) | 0–77.5 % |
| Local | 2 m×2 m plot | Grass cover (%) | 0–77.5 % |
| Local | 2 m×2 m plot | Rock cover (%) | 0–57.5 % |
| Local | 2 m×2 m plot | Height of tallest vegetation (cm) | 9.0–136.5 cm |
| Local | 2 m×2 m plot | Temperature | 16–32 °C |
| Local | 2 m×2 m plot | No. of flowers | 0–370 |
| Local | 1 m×1 m plot | Flower volume (cm ³) | 0–8161 cm ³ |
| Local | 25 m radius plot | Canopy cover (%) | 1.8–89.6 % |
| Local | 25 m radius plot | No. of flowers | 11–1070 |
| Local | Gardens within property | Vegetable garden area | 1.44–288 m ² |
| Local | Gardens within property | Ornamental flower area | 15.3–450.95 m ² |
| Local | Gardens within property | Native ornamental flower area | 0–450.95 m ² |
| Local | Gardens within property | Non-native ornamental flower area | 0–110.69 m ² |
| Landscape | 500 m, 1 km, and 2 km | Water (%) | 0–20 % |
| Landscape | 500 m, 1 km, and 2 km | Wetlands (%) | 0–5 % |
| Landscape | 500 m, 1 km, and 2 km | Open area (%) | 4–51 % |
| Landscape | 500 m, 1 km, and 2 km | Developed area (%) | 22–95 % |
| Landscape | 500 m, 1 km, and 2 km | Forest (%) | 0–45 % |
| Landscape | 500 m, 1 km, and 2 km | Grassland (%) | 0–2 % |
| Landscape | 500 m, 1 km, and 2 km | Crops (%) | 0–19 % |

Results

We collected 693 bee individuals. We found 280 individuals in non-native gardens and collected 413 individuals in native plant gardens (Table S3). The most abundant genera collected included *Lasioglossum* (159 individuals), *Bombus* (134), and *Apis* (75). The four most common bee species in non-native gardens were *Apis mellifera* (10.3 % of individuals), *Bombus bimaculatus* (5.7 %), *Bombus impatiens* (4.4 %), and *Halictus ligatus* (4.4 %). In native plant gardens, the three most common species were *Bombus impatiens* (15.3 % of individuals), *Apis mellifera* (14.0 %), *Ceratina dupla* (8.0 %), and *Agapostemon virescens* (7.6 %). The results from our linear mixed models showed that bee abundance was significantly higher in native gardens than non-native gardens (Fig. 2a; $F_{1,7}=6.178$, $P=0.042$). Likewise, abundance of native bees was higher in the native plant gardens than in non-native gardens (Fig. 2b; $F_{1,7}=17.624$, $P=0.004$). Cavity-nesting bee abundance was higher in native gardens than in non-native gardens (Fig. 2c; $F_{1,7}=8.470$, $P=0.023$), but ground-nesting bee abundance did not differ in native and non-native gardens (Fig. 2d; $F_{1,7}=3.265$, $P=0.114$).

We collected 66 species of bees: 53 in non-native plant gardens and 54 in native gardens. The three genera with the largest number of species were *Lasiglossum* (16 species), *Megachile* (7), and *Bombus* (5). We examined mean and cumulative species richness in the gardens with and without native plants. Our linear mixed models did not show any significant difference in mean species richness per site, across all bees collected, between native and non-native gardens (Fig. 2a; $F_{1,7}=3.295$, $P=0.112$). There were no significant differences between mean richness of native bees in native and non-native gardens (Fig. 2b; $F_{1,7}=3.564$, $P=0.101$). Cavity-nesting bee richness was higher in native than in non-native gardens (Fig. 2c; $F_{1,7}=10.548$, $P=0.014$), but ground-nesting bee richness did not differ between native and non-native gardens (Fig. 2d; $F_{1,7}=0.346$, $P=0.575$). We generated three species accumulation curves to compare cumulative richness of bees collected with netting, pan trapping, or with all methods combined. For each of the accumulation curves, the 95 % confidence intervals overlapped, indicating there were no differences in species richness of bees between native and non-native gardens (Fig. 3a, b, c). However, for native bees, there were near-significant differences in cumulative richness with a slightly higher number of native bee species in sites without native plants compared to those with native plants.

Bee community composition significantly differed with habitat type (Fig. 4). Composition was more similar among sites of the same habitat type than between habitat types (NMDS stress=0.2805, ANOSIM; $P=0.047$). There was however no significant difference in the scatter of points; non-native and native sites had a similar spread of points indicating that community composition was similarly varied among sites of the same habitat type (NPMANOVA; $F=1.393$, $P=0.081$). From examining the species overlaid on the NMDS, it appears as if *Apis mellifera* clustered near a

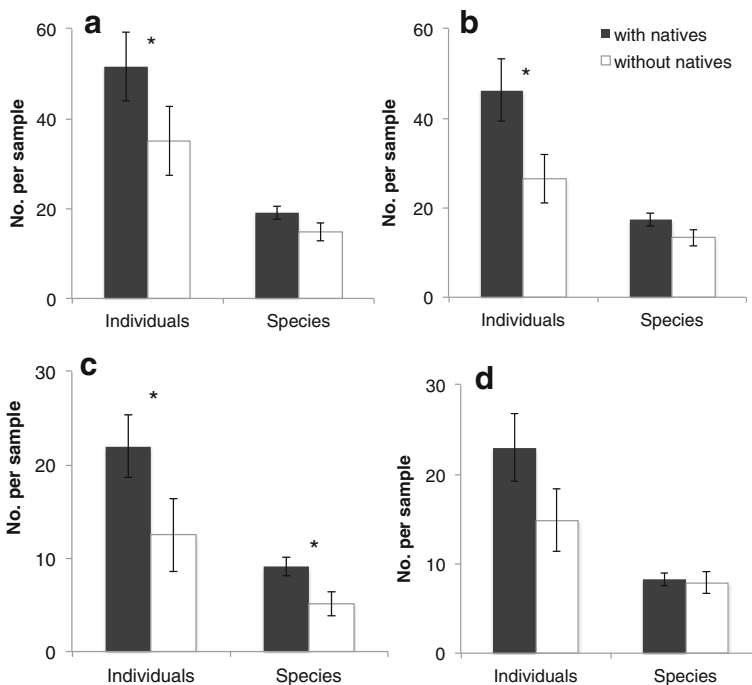
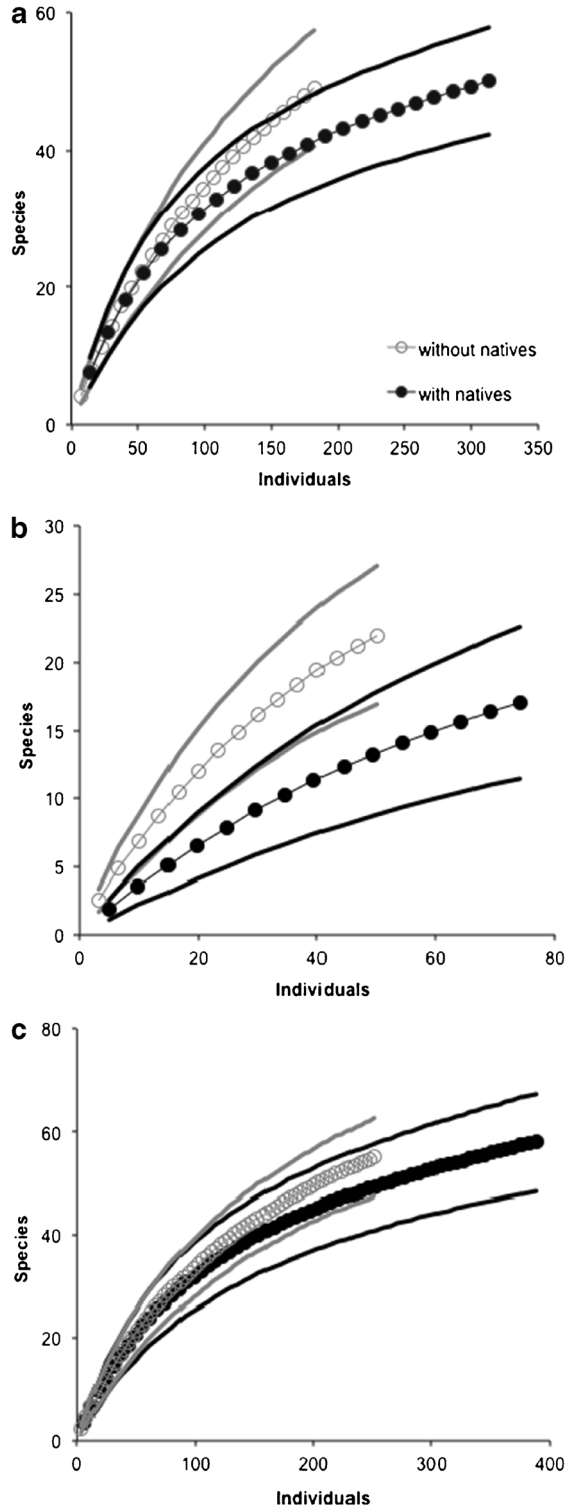


Fig. 2 Mean numbers of individuals and species of **a** all bees, **b** native bees, **c** cavity-nesting bees, and **d** ground-nesting bees per sample in gardens with (black bars) and without (white bars) native plants. Error bars show standard error, and asterisks indicate significant differences between native and non-native gardens

Fig. 3 Species accumulation curves for species and individuals of bees collected in backyard gardens throughout northwestern Ohio show **a** bees collected from netting, **b** bees collected from pan trapping, and **c** bees collected from netting, pan trapping, and direct observation. *Black circles* represent native plant gardens and *open gray circles* represent non-native plant gardens. *Lines* show 95 % CI for observed or estimated richness for symbols of the same color



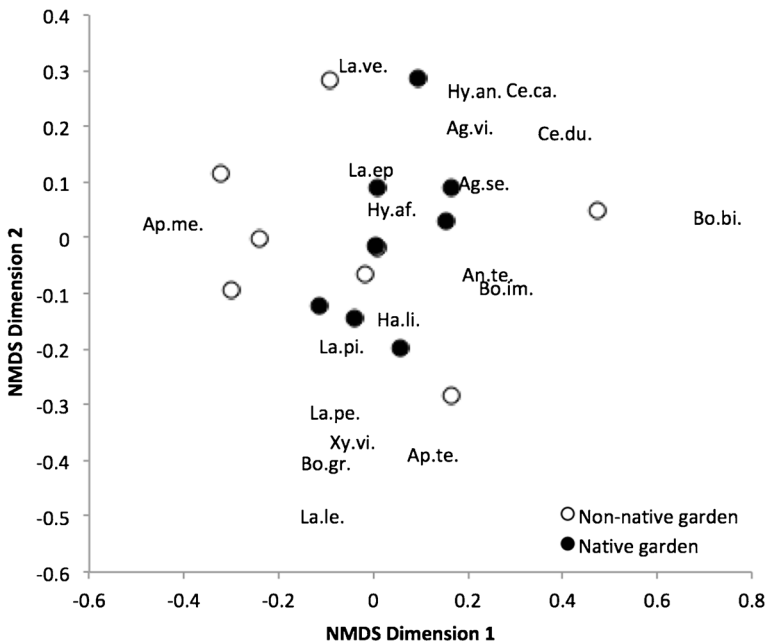


Fig. 4 Non-metric multidimensional scaling (NMDS) analysis examining species similarity of bees collected from backyard garden sites with native plants and without native plants in northwestern Ohio. Each point represents a backyard garden. Black circles represent native gardens, and open gray circles represent non-native gardens. Codes show species collected from more than 10 individuals (Ag.se. = *Agapostemon sericeus*, Ag.te. = *Agapostemon texanus*, Ag.vi. = *Agapostemon virescens*, An.te. = *Anthophora terminales*, Ap.me = *Apis mellifera*, Bo.bi. = *Bombus bimaculatus*, Bo.gr. = *Bombus griseocollis*, Bo.im = *Bombus impatiens*, Ce.al. = *Ceratina calcarata*, Ce.du. = *Ceratina dupla*, Ha.li. = *Halictus ligatus*, Hy.af. = *Hylaeus affinis*, Hy.an. = *Hylaeus annulatus*, La.ep. = *Lasioglossum ephialtum*, La.le. = *Lasioglossum leucocomum*, La.pe. = *Lasioglossum pectorale*, La.pi. = *Lasioglossum pilosum*, La.ve. = *Lasioglossum versatum*, Xy.vi. = *Xylocopa virginica*)

group of non-native plant sites, and that several species of *Agapostemon*, *Ceratina*, *Halictus*, *Hylaeus*, and *Lasioglossum* clustered near the native plant sites.

We found that characteristics of backyards and the surrounding land cover types varied between sites, but not necessarily between native and non-native gardens (Table 2). Although native plant gardens had more native plants, overall floral abundance did not differ between native and non-native gardens ($F_{1,7}=0.630$, $P=0.809$).

Overall bee abundance and richness were correlated with several local characteristics of the backyard gardens, but not with any land cover characteristics. Bee abundance and richness in netting samples were not correlated with any of the predictor variables ($P>0.05$). For observations, bee abundance was significantly higher with higher floral abundance, where woody plants provided more ground cover, in backyards with larger vegetable gardens, and where vegetation was taller (Fig. 5a). Bee richness for observations increased where floral abundance was higher, and where vegetation was taller (Fig. 5b). For bees caught in pan traps, both abundance and richness were higher in backyards with less grass cover, and abundance was also higher in yards with more mulch cover (Fig. 5c, d).

We found that abundance and richness of cavity- and ground-nesting bees were correlated with local backyard and landscape land cover characteristics. Cavity-nesting bee abundance was positively correlated with local factors such as increases in herbaceous vegetation cover, floral

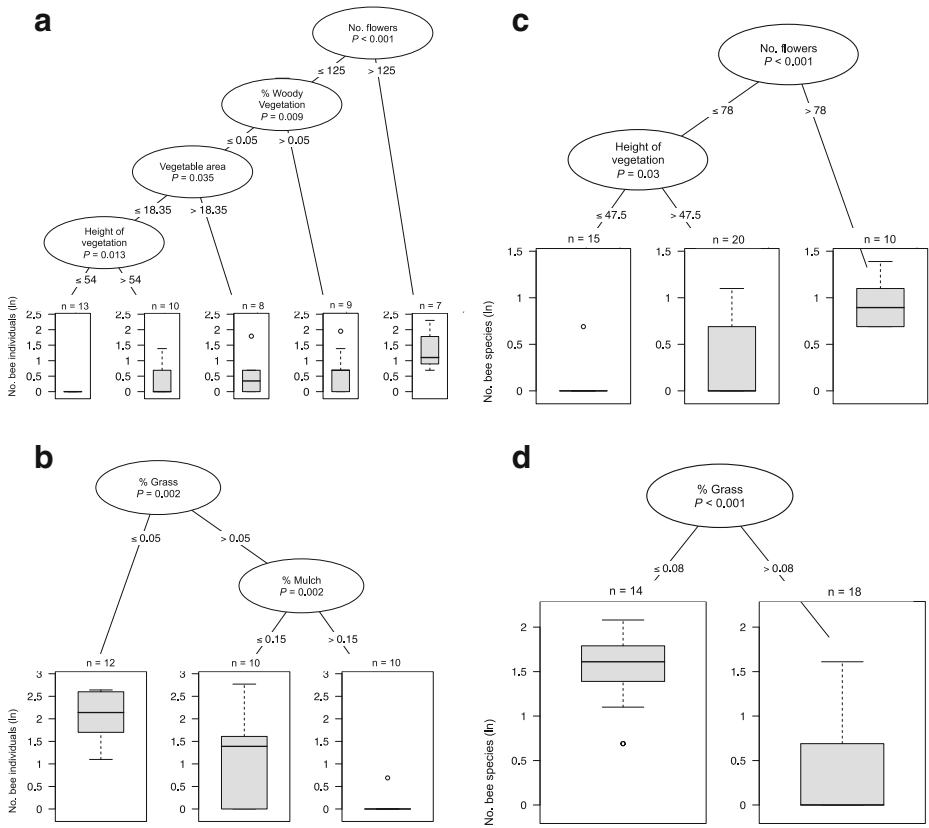


Fig. 5 Conditional inference tree showing significant predictors of bee abundance and richness in backyard gardens in northwestern Ohio. *Panels* show **a** bee abundance in netting samples, **b** bee richness in netting samples, **c** bee abundance in observations, **d** bee richness in observations, **e** bee abundance in pan traps, and **f** bee richness in pan traps. *Encircled* are the biologically significant ($P < 0.05$) predictors of bee abundance or richness in a hierarchical ranking. *Box plots* include the inner quartiles (grey box), the median values (solid black line), and $1.5 \times$ the inner quartiles (error bars) associated with each string of predictor variables. Plots at each terminal node show the data for number of sites (n) predicted by those variables

abundance, and decreases in grass cover (Table 3). Cavity-nesting bee abundance also positively correlated with landscape factors including increases in open area and forest (Table 3). Cavity-nesting bee species richness responded only to local factors and was higher in sites with lower grass cover, taller vegetation, higher floral abundance, and with larger vegetable gardens (Table 3). Ground-nesting bee abundance was positively correlated with local factors and increased in sites with more woody vegetation, mulch, and less grass (Table 3). Ground-nesting bee abundance correlated with two landscape factors increasing in sites with higher forest cover within 2 km, and with wetlands within 1 km (Table 3). Ground-nesting bee species richness was higher in sites with taller vegetation, larger gardens, and less grass cover (Table 3).

Discussion

Our first research question aimed to address whether native and non-native gardens differ in terms of bee abundance and richness. We found more bee individuals in native gardens, and a

Table 3 Local and landscape factors that positively correspond to bee species richness and abundance of ground nesting and cavity nesting bees

| Nesting type | Variable tested ^a | Collection method ^b | Factor | Threshold | Local or landscape | <i>P</i> |
|--------------|------------------------------|--------------------------------|--------------------------|-----------------------|--------------------|----------|
| Cavity | A | N | Herbaceous cover (%) | >62.5 % | local | 0.002 |
| Cavity | A | O | Floral abundance | >125 | local | 0.002 |
| Cavity | A | P | Grass cover (%) | <5 % | local | 0.007 |
| Cavity | A | N | Open area within 1 km | >14 % | landscape | 0.028 |
| Cavity | A | O | Forest within 500 m | >6 % | landscape | 0.003 |
| Cavity | R | N | Grass cover (%) | <17.5 % | local | 0.01 |
| Cavity | R | O | Vegetation height | 106.5 cm | local | 0.042 |
| Cavity | R | O | Floral abundance | >74 | local | 0.006 |
| Cavity | R | P | Grass cover (%) | <5 % | local | 0.003 |
| Cavity | R | O | Vegetable garden size | >28.76 m ² | local | <0.001 |
| Ground | A | O | Woody cover (%) | >15 % | local | 0.003 |
| Ground | A | O | Mulch cover (%) | >5 % | local | 0.033 |
| Ground | A | P | Grass cover (%) | <5 % | local | 0.006 |
| Ground | A | O | Forest area within 2 km | >9 % | landscape | 0.032 |
| Ground | A | P | Wetland area within 1 km | >0 % | landscape | 0.031 |
| Ground | R | O | Vegetation height | 65 cm | local | 0.011 |
| Ground | R | O | Vegetable garden size | >18.35 m ² | local | 0.011 |
| Ground | R | P | Grass cover (%) | <7.5 % | local | 0.008 |

^a *A* bee abundance, *R* bee species richness

^b *N* netting, *O* observation, *P* pan trapping

The threshold shows the value above or below which bee abundance or species richness increased according to conditional inference trees

significantly higher abundance of native bees in native gardens than in non-native gardens. We did not find significantly more bee species, overall, in native plant gardens. However, our finding that native plants promote bee abundance is congruent with at least one other study that has focused specifically on the importance of native plants to bees and bee diversity in urban areas. Pawelek et al. (2009) found higher bee abundance in a community garden in California augmented with native plants, and increases in bee richness from 5 to 31 species within 3 years of planting natives. Likewise, 78 % of native plants and 9.5 % of exotic plants attracted bees in residential neighborhoods of Berkeley and Albany, California, thus further providing support that native plants might positively influence bee presence and abundance (Frankie et al. 2005). In contrast to our results, Matteson and Langellotto (2011) found that planting native plants in New York City community gardens did not affect pollinators, and that exotic plant species attracted a higher number of bees (Matteson and Langellotto 2011). This difference may have been due to the characteristics of the native plant gardens used in each study. In our study, we sampled in native plant gardens that were planted at least 2 years prior to the experiment, and at least 48 % of the flower area was compared of native plants. Matteson and Langellotto (2011) planted native plants within non-native community gardens 13 months prior to sampling, and only planted 70 native plants within a 10 m² area of the non-native plant garden, so the gardens contained less than 30 % native plants. The small size and young age of the native plant gardens used may explain the failure to increase bee species richness. Although we attribute differences we observed to presence of native plants, it is possible that

other characteristics of backyard management (e.g., herbicide or fertilizer use, type of lawn mower, etc.) may also differ between households that have native plants and those that do not, so we cannot rule out that those factors may have contributed to observed differences in bee communities. Further, estimates of floral abundance (counted with 25 m of the observation point) did not provide an exact number of flowers per species within the observation area thereby affecting our results. Notable is that we did not sample the full bee community as our accumulation curves did not reach asymptotes, however, adding various sample methods improved the overall species capture. With more sampling, the overall results may have changed. Nonetheless, our current results demonstrate that native plants may increase bee abundance, and specifically native bee abundance in backyard gardens, thereby promoting bee communities in urban areas.

We also determined that the composition of bee species was significantly different in the native vs non-native gardens, thus the native plant gardens attracted a unique group of bees not found in non-native gardens. In our NMDS plot, smaller, native bees (<11 mm) (such as members of the genera *Agapostemon*, *Ceratina*, *Halictus*, *Hylaeus*, and *Lasioglossum*) were clustered together near native plant gardens whereas the larger bees (>11 mm), including *Apis mellifera*, were spaced further apart, and closer to clumps of non-native gardens. Other studies that have examined community composition in urban areas have found differences in bee composition depending on habitat type studied, as well as the particular features of the habitats studied (McIntyre and Hostetler 2001; Neame et al. 2013). In addition, urbanization can influence the pollinator-plant networks altering the community of bees that are visiting certain floral resources (Geslin et al. 2013). Winfree et al. (2007) found that bees tend to cluster together based on functional traits such as body size, and nesting preference. Additionally, Cane et al. (2006) found that dietary breadth was correlated with size of fragments in urban areas. For example, ground-nesting specialist bees species preferred to forage in much larger fragments, while ground nesting generalist species foraged in both large and small fragments (Cane et al. 2006). These changes in community composition depending on the presence of native plants could have implications for bee conservation and for pollination services.

Our second question aimed to address which local and landscape characteristics of gardens correlated with changes in abundance and richness of all bees, and of certain groups of bees. Seven characteristics of the backyard gardens influenced abundance and richness of bees overall, and for cavity-nesting and ground-nesting bees. Grass cover was negatively correlated with abundance and richness of all bees. In our study, the area of grass negatively correlated with increases in herbaceous cover, which may signify fewer floral resources. In addition, although we did not measure for presence or frequency of application, in general, turf grass may be treated with insecticides that may negatively impact bees (Larson et al. 2013). Likewise, herbaceous cover was positively correlated with abundance of cavity-nesting bees sampled in netting, and herbaceous cover may decrease as grass cover increases in backyards. Ground-nesting bees, in particular, are strongly affected by urbanization due to changes in vegetation from natural plants to grass lawns and an alteration of surface soils (Cane et al. 2006). Floral resources were important for both abundance and richness of all bees and cavity-nesting bee abundance and richness. Woody vegetation was positively correlated with abundance of all bees, and of ground-nesting bees sampled from observations. Woody plants can provide nesting sites for bees and therefore may be important in promoting bee diversity (Cane et al. 2006). Bees can either excavate nests from the wood, or occupy holes created by other wood-boring insects. Bee abundance in pan traps, and numbers of ground-nesting bees netted was higher in sites with more mulch. Because we defined mulch as areas covered with a thin layer of leaves, bark, or compost, our results are similar to previous findings that ground-nesting bees prefer either bare soil or a thin layer of leaf litter to construct their nests (Frankie

et al. 2009; Welzel 2011). Larger vegetable gardens supported higher bee abundance, and a greater number of cavity- and ground-nesting bee species. Many of the fruits and vegetables planted within each of our vegetable gardens are dependent on bee pollination, so larger vegetable gardens may contain more bee-attracting flowers. Finally, bee richness overall, and for cavity- and ground-nesting bees increased with height of the vegetation. Likewise, in grasslands, bee richness correlates with vegetation height (Kruess and Tschamtkke 2002; Ockinger and Smith 2007). It is also possible that taller vegetation facilitated easier viewing of bees. Interestingly, we only documented certain results for bees found with one or another sample method, but as the sample method largely defines the specific community collected, it is not all that surprising that some results were method-specific.

Other local factors not measured in our study may promote bee diversity in urban areas. For example, bee diversity increases in urban sites with abandoned rodent nests that can act as nesting sites (Goulson et al. 2008; McFrederick and LeBuhn 2006). Further, planting flowers that will bloom successively throughout the season provides consistent nectar sources (Pawelek et al. 2009; Tuell et al. 2008), and therefore may promote bee diversity as different bee species have different seasonal foraging behaviors (Wojcik et al. 2008). For example, in late spring, wild bees are more abundant in urban areas of Vancouver, whereas honeybees are more commonly found in the same areas during late summer (Tommasi et al. 2004). In our study, we did not find that bee abundance or richness varied with plant richness. However, previous studies have found that bee richness, and specifically native bee richness, positively correlates with plant richness in pastures in Costa Rica (Brosi et al. 2008) and in urban gardens in San Luis Obispo, CA (Pawelek et al. 2009).

Landscape characteristics may affect bee communities, but we only observed influences of surrounding land cover on ground- and cavity-nesting bee abundance, not on bee abundance and richness generally, or for richness of ground- and cavity-nesting bees. Abundance of cavity-nesting bees was higher with more open space within 1 km. Previous research that focused on the correlation between bee richness and open areas, where natural habitat was replaced, have found similar results. For example, Matteson et al. (2008) found an increase in cavity-nesting bees in urban community gardens compared to natural habitats. Further, cavity-nesting bee abundance increased in desert habitat fragmented by urban areas, compared to continuous desert fragments (Cane et al. 2006). These open areas may have a higher diversity of cavity-nesting bees because there are both natural and man made resources in which to build nests. Ground-nesting bees were more abundant with greater wetland cover within 1 km of each sampling point. This result has also been shown in Poland, where wet meadows maintain a high diversity of native bees (Moron et al. 2008). Also, 74 % of the bees collected in the wet meadows were ground-nesting bees. We also found that abundance of both cavity-nesting and ground-nesting bees was positively associated with forest cover, but at two different spatial scales. Cavity-nesting bees were positively correlated with forest cover in 500 m buffers, and ground-nesting bees were positively correlated with forest cover in 2 km buffers. The cavity-nesting bees may have responded to features at a smaller spatial scale for a few reasons. First, cavity-nesting bees create nests in houses, fences, and woody vegetation, indicating that they might nest closer to floral resources, and so they may not be as affected by urbanization as other nesting guilds (Cane et al. 2006). Second, bee foraging distance is related to body size; smaller bees forage closer to nests whereas larger bees disperse great distances of up to 10 km from nests (Goulson and Stout 2001; Gathmann and Tschamtkke 2002). Two of the common cavity-nesting bee genera we collected, *Ceratina* and *Hyleaus* are smaller bees (4.5–8 mm long). In contrast, common ground-nesting bee genera collected such as *Bombus* (15–23 mm long) and *Agopostemon* (10–11 mm long) are larger, and may forage further. *Bombus* spp. may forage >10 km from nests over several days (Goulson and Stout 2001; Hines and Hendrix

2005). Thus, wetlands and forests at greater distances from the study sites may provide more opportunities for bumble bees to locate floral resources. Generally, pollinator diversity increases with increasing landscape heterogeneity (Jha and Vandermeer 2010; McFrederick and LeBuhn 2006; Thies and Tschamtkke 1999), and with increasing proximity to riparian forests (Kremen et al. 2004). Likewise, urban gardens near natural, unmodified habitats (e.g. forest fragments and meadows) support more bee diversity (McFrederick and LeBuhn 2006). Thus our results are largely consistent with previous studies except that we only found landscape influences on specific guilds of bees.

Our final research question addressed whether bee abundance and richness was more strongly influenced by local or landscape characteristics. Overall, we found stronger correlations of local rather than landscape effects on bee communities, for all bees, and for cavity- and ground-nesting bees. Local factors were always the strongest predictors of abundance and richness where both local and landscape factors appeared in conditional inference trees. Although previous studies have documented the importance of both local and landscape factors for bee abundance, few have examined the relative impacts. Jha and Vandermeer (2010) also found that local factors better predicted bee abundance and richness in a tropical agricultural landscape. Steffan-Dewenter et al. (2002), found that solitary bees, bumble bees, and honeybees responded differently to local and landscape factors. Solitary bee richness and abundance were most affected by the percentage of semi-natural habitat on a local scale (<750 m radius), whereas honeybees and bumble bees were more affected by the percentage of semi-natural habitat at large landscape scales (3,000 m radius).

Our results show that modifications to backyard gardens can potentially increase bee abundance, and based on our findings, we have several recommendations that may be useful for increasing native bee abundance in urban environments. First, planting flowers that are native to the region near vegetable gardens might increase bee abundance, and could potentially increase the richness of cavity-nesting bees. Second, replacing grass with flower gardens and vegetable gardens may provide more floral resources for bees, therefore increasing bee diversity. Finally, planting a wide variety of plant species within backyard gardens (including both ornamental and crop plants) might attract a higher diversity of bees. Although landscape factors also influenced abundance and richness of cavity- and ground-nesting bees, local factors, that can be more easily manipulated by homeowners more strongly affected these bees. Thus, taken together, these steps may attract more native bees and promote urban bee diversity in general.

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