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Permalink

https://escholarship.org/uc/item/68p8m8n2

Journal

Environmental Entomology, 45(3)

ISSN

0046-225X

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Publication Date

2016-06-01

DOI

10.1093/ee/nvw025

Peer reviewed

OXFORD

Community and Ecosystem Ecology

Landscape and Local Correlates of Bee Abundance and Species Richness in Urban Gardens

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Abstract

Urban gardens may preserve biodiversity as urban population densities increase, but this strongly depends on the characteristics of the gardens and the landscapes in which they are embedded. We investigated whether local and landscape characteristics are important correlates of bee (Hymenoptera: Apiformes) abundance and species richness in urban community gardens. We worked in 19 gardens in the California central coast and sampled bees with aerial nets and pan traps. We measured local characteristics (i.e., vegetation and ground cover) and used the USGS National Land Cover Database to classify the landscape surrounding our garden study sites at 2 km scales. We classified bees according to nesting type (i.e., cavity, ground) and body size and determined which local and landscape characteristics correlate with bee community characteristics. We found 55 bee species. One landscape and several local factors correlated with differences in bee abundance and richness for all bees, cavity-nesting bees, ground-nesting bees, and different sized bees. Generally, bees were more abundant and species rich in bigger gardens, in gardens with higher floral abundance, less mulch cover, more bare ground, and with more grass. Medium bees were less abundant in sites surrounded by more medium intensity developed land within 2 km. The fact that local factors were generally more important drivers of bee abundance and richness indicates a potential for gardeners to promote bee conservation by altering local management practices. In particular, increasing floral abundance, decreasing use of mulch, and providing bare ground may promote bees in urban gardens.

Key words: agriculture, Apiformes, biodiversity, California, urbanization

Urbanization is a major threat to natural habitat and to biodiversity. Half of the world's population lives in urban areas, and that percentage is expected to increase as the human population continues to grow (Pickett et al. 2013). Globally, the number of people in urban areas has increased rapidly—from about 2% of the population in 1800 to 12% in 1900, and about 50% in 2014 (Bloom 2011, US Census Bureau 2014). Certain global regions sustain even higher urban populations with, for example, >80% of the U.S. population living in urban areas (US Census Bureau 2014). Urbanization results in increases in concrete and buildings, destruction and fragmentation of natural habitat, and loss of suitable areas for wildlife (McIntyre et al. 2001, Seto et al. 2012). Urban growth is considered the type of habitat loss with the most longevity, resulting in the largest, most permanent loss of species (McKinney 2002). In addition, the importance of biodiversity is often overlooked in land use planning for urban areas resulting in further species loss, and subsequent impacts for ecosystem services (Rey-Benayas et al. 2009).

Despite threats to biodiversity created by urbanization, certain urban habitats support biodiversity and ecosystem services. Green spaces within urban areas with significant amounts of vegetation can provide a refuge for species of plants, animals, and microbes (Kong et al. 2009, Lin et al. 2015). Thus, diversity of vertebrates and invertebrates can be conserved through the maintenance of urban green spaces, including, but not limited to, parks, backyard gardens, and small-scale agricultural systems (McKinney 2002, Pardee and Philpott 2014). Local characteristics, such as garden size, floral diversity, and vegetation complexity, are important predictors of invertebrate species richness in urban areas (McGeoch and Chown 1997, Frankie et al. 2005, Matteson and Langellotto 2010, Lin et al. 2015). Yet, urban habitat fragments might be too small or too disconnected from other patches to preserve biodiversity long-term, and the impacts of local habitat enhancements on biodiversity are contingent on surrounding landscape quality (e.g., Tscharntke et al. 2005). Thus, it is also necessary to examine the landscape surroundings of these habitat patches to assess the degree to which gardens add to connectivity across the landscape (Savard et al. 2000, Rudd et al. 2002). In studies where landscape characteristics are considered, connectivity and patch size are important for preserving urban biodiversity (Rudd et al. 2002, Goddard et al. 2010). Further, one study shows that the degree to which

improvements to local resources increase beneficial insects depends on the amount of impervious cover in the surrounding urban landscape (Bennett and Gratton 2012). Yet, landscape factors are not always important for predicting invertebrate abundance and richness in urban areas (e.g., Williams and Winfree 2013), and other factors such as ethnicity and income may be additionally important for predicting biodiversity (Clarke and Jenerette 2015).

Because urban gardens are used for food production, conserving biodiversity of pollinators, such as bees, is especially important. Bees and other pollinators increase the production of 39 of the 57 major food crops in the world; 13 of those crops require animal pollination for fruit set (Klein et al. 2007). In addition, increasing bee diversity often results in increases in fruit set in species that rely on bee pollination (Kremen et al. 2002, Klein et al. 2003). Thus, understanding the drivers of bee abundance and bee species richness in urban vegetable gardens is a crucial aspect of preserving the pollination services provided in urban systems. Bees can be limited by the availability of suitable nesting sites and floral resources in urban and natural systems (Gathmann and Tscharntke 2002, Frankie et al. 2005), resulting in nesting sites that may be separated from foraging locations. Bees, depending on body size, will forage up to 10 km or more from the nest (with most species foraging <2 km), which makes understanding both landscape and local drivers of bees critical (Greenleaf et al. 2007).

In this study, we examined bee abundance and species richness in urban vegetable gardens in the California central coast region. Specifically, we aimed to answer the following questions: 1) How many species of bees are found within urban gardens in the California central coast?, 2) Which local and landscape features of gardens correlate with abundance and species richness of bees in urban gardens and do local or landscape predictors more frequently predict abundance and richness of bees?, 3) Which local and landscape features of gardens correlate with abundance and richness of bees with different nesting habits and do local or landscape factors more frequently predict abundance and richness of bees with different nesting habits?, and 4) Which local and landscape features of gardens correlate with abundance and richness of different sized bees and do local or landscape factors more frequently predict abundance and richness of different sized bees?

Materials and Methods

Study Sites
We studied bees in urban gardens in the central coast region of California between May and September 2013. We selected 19 gardens in Monterey (6 gardens), Santa Cruz (7 gardens), and Santa Clara (6 gardens) Counties for field research. Each garden is an urban community garden (managed either in allotments or collectively) and gardens ranged in size from 444 m^2 to 15,525 m^2. Each garden contained vegetable crops and had been in production for between 4–46 yr. All gardens were separated from each other by a minimum of 2 km.

Local Factors
In each garden, we collected data on vegetation and ground cover factors. We quantified 38 local site characteristics in plots surrounding areas where bees were collected across three (nested) spatial scales (100 by 100 m^2, 20 by 20 m^2, and 1 by 1 m^2). Data in 100- by 100-m plots were collected once, in September, and data from 20- by 20-m and 1- by 1-m plots were collected once per month between May and September. In the 100- by 100-m plots, we counted all

trees (>30 cm circumference at breast height [cbh]) and quantified percent area of 1) concrete and buildings, 2) mulch, 3) bare ground, 4) grass, 5) woody vegetation, and 6) herbaceous or weedy vegetation. In the 20- by 20-m plots, we sampled canopy cover with a concave spherical densiometer at the center of each plot, and 10 m to the N, S, E, and W of the center. We counted trees >30-cm cbh, shrubs <2 m tall, the number of trees and shrubs in flower, measured the height of all trees, and calculated the number of woody plant species in each plot. We randomly placed four 1- by 1-m plots within the 20- by 20-m plots, in which we counted number of herbaceous plant species, counted the number of white, red, yellow, blue, violet, and pink flowers, the total number of flowers, measured the height of the tallest herbaceous vegetation, and estimated the percent cover of 1) bare ground, 2) grasses, 3) herbaceous plants, 4) rocks or wood panels, 5) leaf litter, 6) mulch, and 7) concrete. We also measured the size of each garden.

Landscape Analysis
We used a geographic information system to investigate land-cover types surrounding each garden study site. We used land-cover data from the 2011 National Land Cover Database (NLCD, 30 m resolution; Homer et al. 2015) and calculated the percentage of land-cover types in buffers surrounding each study site. Following the methods of Jha and Kremen (2013), we divided land-cover types into six categories based on the perceived level of nesting resistance: 1) low intensity urban (<50% impermeable surface area; NLCD values 21 and 22), 2) medium intensity urban (50–79% impermeable surface area; NLCD 23), 3) high intensity urban (≥80% impermeable surface area; NLCD 24), 4) forest (evergreen, deciduous, and mixed forest; NLCD 41, 42, and 43) 5) grassland (NLCD 71), and 6) crops (NLCD 81 and 82). Other land-cover types in the surrounding areas (open water 11; scrubland 51, 52; wetlands 90, 95) accounted for <5% of the landscape and were not included in analysis. We assessed the percent of each land-cover type in 2-km buffers around each study site with spatial statistics tools in ArcGIS v. 10.2.

Bee Sampling
We sampled bees using elevated pan traps and aerial nets once per month between May and September 2013. We combined these two sampling methods to effectively attain an accurate representation of the bees present in the garden (Grundel 2011). We built the pan traps using 400-ml plastic bowls (yellow, white, and blue) painted with Clear Neon brand clear UV spray paint, to increase the trap's visibility, and glued each bowl to a PVC coupler with multipurpose cement. On trapping days, we placed three 1-m tall PVC pipes in the ground in a triangle formation, 5 m apart within the 20- by 20-m plots, and placed one bowl of each color on top of pipes (Tuell and Isaccs 2009). We placed pan traps once per month between 8–9 a.m. and collected traps between 3–5 p.m. We filled bowls with a water and dish soap mixture, ~300 ml of water and 4ml dish soap. At collection time, we emptied contents of each trap into containers for transport to the lab where we later separated the bees from the other insects. We placed bees in vials containing 70% ethyl alcohol or immediately pinned and dried bees for identification.

We also sampled bees using aerial nets in each site once per month. We actively searched for and captured bees in nets for a total of 30 min per site between 8:30 a.m.–4:30 p.m. The 30 min per site did not include handling time, which was on top of the 30 min. Bees were mostly collected on warm, sunny days, but we did not take specific data on wind, temperature, or cloud cover during surveys. Bees

were observed on flowers, within 20 m of and inside the 20- by 20-m plots in each site. Once we observed a bee, it was captured using the aerial net and transported back to the lab for identification. We used online resources (Discover Life 2014) and other dichotomous keys (Roberts 1973a,b; Michener 2007) to identify the bees to family, genus, and species, and also compared bees collected with specimens in the Norris S. Center for Natural History at UCSC. For those bees that we were unable to identify to species, we separated genera into morphospecies. Only data on female bees were used in the data analysis. We classified bee-nesting categories (ground-nesting, cavity-nesting, or parasitic) and body size (small, <7 mm; medium, 7–12 mm; and large, >13 mm) according to Michener (2007). All bee specimens are currently housed in the Philpott Lab at the University of California, Santa Cruz.

Data Analysis

We collected most data over a 5-mo period, but data from 100- by 100-m plots and the landscape were only sampled once. As we did not want to include repeated samples as replicates, we chose to combine data for different sample months. We summed data for bee abundance and richness across the 5 mo, and used cumulative abundance and richness as response variables. For vegetation and ground cover data that were sampled repeatedly across the summer, we averaged values recorded during different months. For 100- by 100-m plots and landscape variables, we used values that were recorded only once. We examined all dependent and explanatory variables for a normal distribution transformed for some variables to meet conditions on normality (e.g., natural-log transformed for all dependent variables, numbers of white, yellow, purple, pink, and total flowers, numbers of trees and shrubs in 20- by 20-m plots, numbers

of trees and shrubs in flower, number of trees in 100- by 100-m plots, and garden size; square root transformed for percent of mulch cover in 100- by 100-m plots, and percent of lawn cover in 100- by 100-m plots).

Because of the large number of explanatory variables, we used two techniques to reduce the number of variables for analysis. First, we examined all variables to see which might have minimal influence on bees due to low values. Rock and wood panel and concrete cover (in 1- by 1-m plots) always covered <5% of the ground and were not included. We never recorded >100 red, orange, green, or blue flowers in a site, and did not include those variables in analysis. We always found fewer than two grass species per plot, and did not include grass richness as a variable. Next, we ran Pearson's correlations on groups of variables. We grouped variables according to biologically relevant groupings including: 1) 1- by 1-m plot characteristics (percent bare soil, grass, herbaceous vegetation, leaf litter, mulch, and height of the tallest herbaceous vegetation), 2) floral variables (white, yellow, purple, pink, and total flowers), 3) herbaceous plant richness variables (crop species richness, ornamental plant species richness, weed richness, and total herbaceous plant richness), 4) woody plant cover characteristics (canopy cover, number of trees and shrubs in 20- by 20-m plots, number of trees and shrubs in flower in 20- by 20-m plots, mean height of trees in 20- by 20-m plots, number of trees in 100- by 100-m plots, and woody cover in 100- by 100-m plots), 5) ground-cover characteristics in 100- by 100-m plots (percent mulch, bare ground, lawn, concrete and buildings, weedy vegetation, and garden size), and 6) landscape variables (low, medium, and high intensity, forest, grassland, and crops). We examined all correlations within groups, and selected the variable with the highest number of correlates and highest

Table 1. Results of variable selection with Pearson's correlations with selected variables, not-selected correlated variables, and the direction of the correlations

Selected variable	Correlated variables	Correlation coefficient	Direction of correlation
Grass cover (1 m)	NA	NA	NA
Leaf litter cover (1 m)	NA	NA	NA
Mulch cover (1 m)	Bare ground cover (1 m)	0.546	−
	Herbaceous plant cover (1 m)	0.742	−
	Height of tallest herbaceous vegetation (1 m)	0.471	−
No. of flowers (1 m)	No. of yellow flowers (1 m)	0.686	+
	No. of white flowers (1 m)	0.92	+
	No. of red flowers (1 m)	0.348	+
	No. of blue flowers (1 m)	0.412	+
	No. of violet flowers (1 m)	0.511	+
	No. of pink flowers (1 m)	0.51	+
Herbaceous plant species richness (1 m)	Crop species richness (1 m)	0.764	+
	Ornamental plant species richness (1 m)	0.601	+
	Weed species richness (1 m)	0.793	+
No. of woody plants (20 m)	Canopy cover (20 m)	0.525	+
	Tree height (20 m)	0.715	+
	No. of trees, shrubs in flower (20 m)	0.827	+
	No. of trees (100 m)	0.471	+
	Woody plant cover (100 m)	0.451	+
Mulch cover (100 m)	NA	NA	NA
Lawn cover (100 m)	NA	NA	NA
Concrete and building cover (100 m)	Weedy plant cover (100 m)	0.621	−
Garden size	Bare ground cover (100 m)	0.479	+
Medium intensity urban (2 km)	Low intensity urban (2 km)	0.565	−
	High intensity urban (2 km)	0.722	+
	Forest (2 km)	0.807	−
	Grassland (2 km)	0.521	−
Crop cover (2 km)	NA	NA	NA

correlation coefficients as the variable to include in subsequent analysis. All correlations recorded were at the $P < 0.05$ level, and the lowest correlation coefficient recorded for significant correlations was 0.348. Selected and correlated variables are presented in Table 1.

We used generalized linear models with the glm function in R (R Development Core Team 2014) to examine relationships between selected explanatory variables and dependent variables. In our analysis, we used total bee abundance, cavity-nesting bee abundance, ground-nesting bee abundance, total species richness, cavity-

Table 2. Bee species collected in urban gardens in the California central coast with netting and pan trapping between May–September 2013

Bee species	Family	Tribe	Nesting	Size
Agapostemon texanus Cresson	Halictidae	Halictini	Ground	M
Andrena sp. 1 F.	Andrenidae		Ground	M
Andrena sp. 2 F.	Andrenidae		Ground	M
Anthophora sp. 1 Latreille	Apidae	Anthophorini	Ground	M
Anthophora sp. 2 Latreille	Apidae	Anthophorini	Ground	M
Apis mellifera L.	Apidae	Apini	Domestic	M
Ashmeadiella sp. 1 Cockerell	Megachilidae	Osmiini	Cavity	M
Bombus sp. 1 Latreille	Apidae	Bombini	Ground	L
Bombus vosnesenskii	Apidae	Bombini	Ground	L
Ceratina sp. 1 Latreille	Apidae	Ceratinini	Cavity	S
Ceratina sp. 2 Latreille	Apidae	Ceratinini	Cavity	S
Ceratina sequoiae Michener	Apidae	Ceratinini	Cavity	M
Coelioxys sp. 1 Latreille	Megachilidae	Megachilini	Parasitic	M
Diadasia sp. 1 Patton	Apidae	Emphorini	Ground	M
Halictus farinosus Smith	Halictidae	Halictini	Ground	M
Halictus ligatus Say	Halictidae	Halictini	Ground	M
Halictus sp. 1 Latreille	Halictidae	Halictini	Ground	S
Halictus rubicundus Christ	Halictidae	Halictini	Ground	M
Halictus tripartitus Cockerell	Halictidae	Halictini	Ground	S
Halictus sp. 2 Latreille	Halictidae	Halictini	Ground	S
Hylaeus mesillae Cockerell	Colletidae		Cavity	S
Hylaeus punctatus Brullé	Colletidae		Cavity	S
Hylaeus rudbeckiae Cockerell and Casad	Colletidae		Cavity	S
Hylaeus sp. 1 F.	Colletidae		Cavity	S
Hylaeus sp. 2 F.	Colletidae		Cavity	S
Hylaeus sp. 3 F.	Colletidae		Cavity	S
Lasioglossum sp. 1 Curtis	Halictidae	Halictini	Ground	M
Lasioglossum sp. 2 Curtis	Halictidae	Halictini	Ground	S
Lasioglossum sp. 3 Curtis	Halictidae	Halictini	Ground	S
Lasioglossum sp. 4 Curtis	Halictidae	Halictini	Ground	M
Lasioglossum sp. 5 Curtis	Halictidae	Halictini	Ground	S
Lasioglossum sp. 6 Curtis	Halictidae	Halictini	Ground	S
Lasioglossum sp. 7 Curtis	Halictidae	Halictini	Ground	S
Lasioglossum sp. 8 Curtis	Halictidae	Halictini	Ground	S
Lasioglossum sp. 9 Curtis	Halictidae	Halictini	Ground	S
Lasioglossum sp. 10 Curtis	Halictidae	Halictini	Ground	S
Lasioglossum sp. 11 Curtis	Halictidae	Halictini	Ground	S
Lasioglossum sp. 12 Curtis	Halictidae	Halictini	Ground	S
Lasioglossum sp. 13 Curtis	Halictidae	Halictini	Ground	S
Lasioglossum sp. 14 Curtis	Halictidae	Halictini	Ground	S
Lasioglossum sp. 15 Curtis	Halictidae	Halictini	Ground	S
Martinapis sp. 1 Cockerell	Apidae	Eucerini	Ground	L
Megachile sp. 1 Latreille	Megachilidae	Megachilini	Cavity	M
Megachile sp. 2 Latreille	Megachilidae	Megachilini	Cavity	M
Megachile sp. 3 Latreille	Megachilidae	Megachilini	Cavity	M
Megachile sp. 4 Latreille	Megachilidae	Megachilini	Cavity	S
Megachile sp. 5 Latreille	Megachilidae	Megachilini	Cavity	S
Melissodes sp. 1 Latreille	Apidae	Eucerini	Ground	L
Melissodes sp. 2 Latreille	Apidae	Eucerini	Ground	M
Osmia sp. 1 Panzer	Megachilidae	Osmiini	Cavity	S
Peponapis pruinosa Say	Apidae	Eucerini	Ground	M
Sphecodes sp. 1 Latreille	Halictidae	Halictini	Parasitic	S
Svastra aegis LaBerge	Apidae	Eucerini	Ground	L
Xylocopa tabaniformis Smith	Apidae	Xylocopini	Cavity	L
Xylocopa varipuncta Patton	Apidae	Xylocopini	Cavity	L

L, large sized bees (>13 mm); M, medium sized bees (7–12 mm); S, small sized bees (<7 mm).

nesting species richness, ground-nesting species richness, and abundance of large, medium, and small bees as dependent variables. We included the following 10 local explanatory variables: grass cover, leaf litter cover, and mulch cover in 1- by 1-m plots, herbaceous plant species richness, number of flowers, number of woody plants in 20- by 20-m plots, mulch cover, lawn cover, concrete and building cover in 100- by 100-m plots, and garden size. We included two landscape explanatory variables—medium intensity urban cover and crop cover within 2 km. We tested all combinations of the 12 different explanatory variables with the 'glmulti' package (Calcagno and de Mazancourt 2012) and selected the top model based on the AICc values. For models where the AICc for the top model was within 1 point of the next best model, we averaged models (up to the top 10 models) with the MuMIn package (Barton 2012) and report conditional averages for significant model factors.

Results

In total, we collected 2,566 bees, including 2,215 females and 351 males. We identified 55 morphospecies, of which *Halictus*

tripartitus Cockerell (38.6% of total individuals captured), *Apis mellifera* L. (34.6%), *Lasioglossum* spp. Curtis (7.67%), and *Bombus vosnesenskii* Radoszkowski (3.61%) were the most common in samples. The most diverse genera collected were *Lasioglossum* Curtis (15 species), *Hylaeus* F. (6 species), and *Halictus* Latreille (6 species). Across all sample months, we collected between 7 and 17 species and 39 and 511 individuals per garden. Among the species we collected, 34 are ground-nesting species, 19 are cavity-nesting species, and 2 are parasitic species (Table 2).

Several local factors were significant correlates of overall abundance and richness of bees. The top three models predicting bee abundance had similar AICc values, and the averaged model included garden size (a variable in all three top models, $P = 0.012$), medium intensity developed land in 2 km (in one model, $P = 0.079$), and the number of woody plants in 20- by 20-m plots (in one model, $P = 0.094$). Bee abundance was significantly higher in larger gardens (Fig. 1a). The best model predicting bee species richness included the number of flowers ($P = 0.013$), garden size ($P < 0.001$), and mulch cover in 100- by 100-m plots ($P = 0.001$). Bee species richness was higher in gardens with more flowers (Fig. 1b), in larger gardens (Fig. 1c), and was lower in gardens with high mulch cover in 100- by 100-m plots (Fig. 1d).
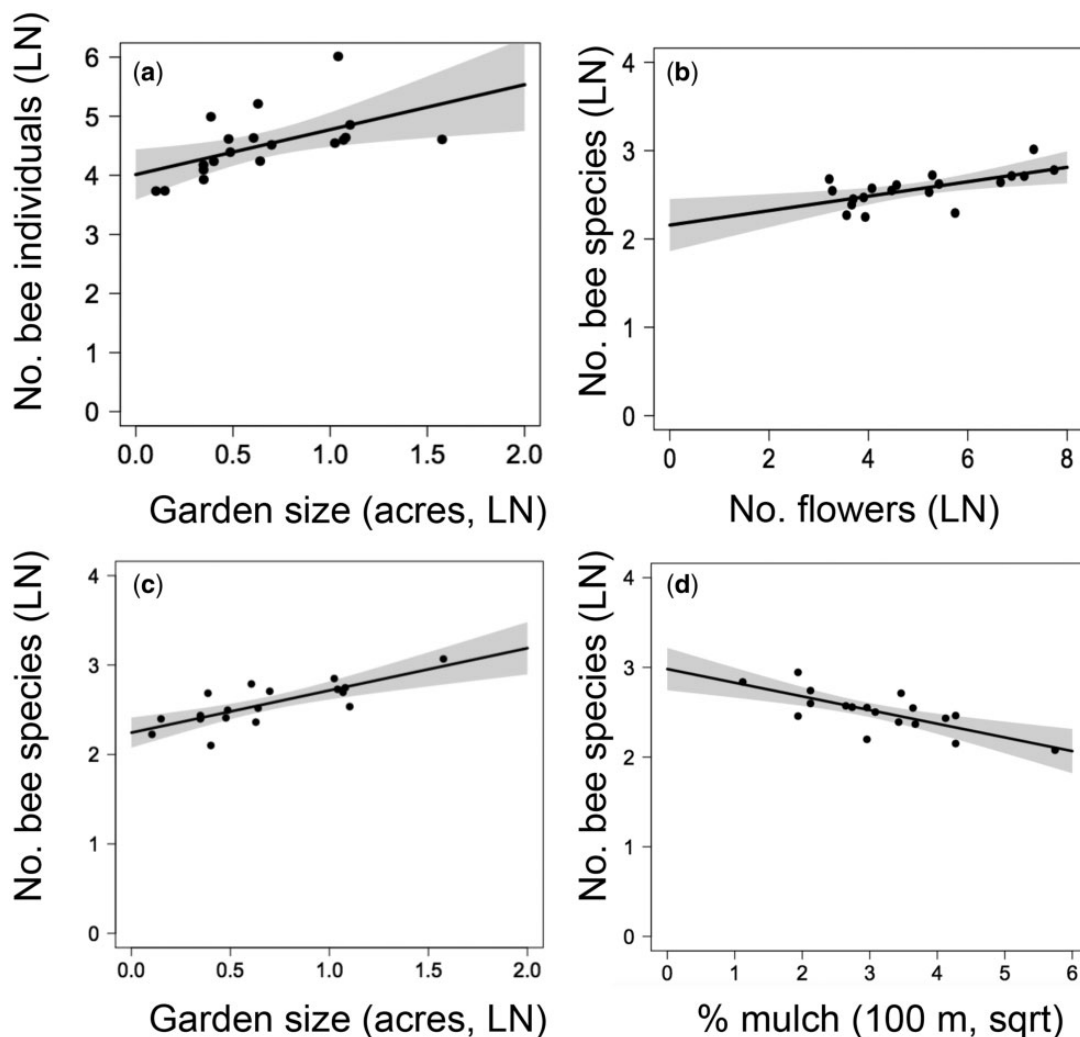

Fig. 1. Relationships between significant factors in generalized linear models and bee abundance and richness for bee abundance (**a**) and bee species richness (**b–d**). All factors were significant at the $P < 0.05$ level. Each dot represents an urban garden study site, the lines show the best fit, and the grey area cover confidence bands based on the generalized linear models.

Models predicting the abundance and richness of both cavity-nesting and ground-nesting included both local and landscape factors, but local factors were the only significant correlates. Cavity-nesting bee abundance was best predicted by leaf litter cover in 1- by 1-m plots ($P = 0.013$), and was significantly higher in sites with more leaf litter (Fig. 2a). The top 10 models predicting cavity-nesting bee species richness were similar according to AICc scores, and the averaged model included herbaceous plant species richness (included in 7 of the top 10 models, $P = 0.048$), mulch cover in 100- by 100-m plots (in seven models, $P = 0.029$), garden size (in four models, $P = 0.039$), leaf litter cover in 1- by 1-m plots (in four models, $P = 0.079$), concrete and building cover in 100- by 100-m plots (in one model, $P = 0.071$), number of flowers (in one model, $P = 0.072$), and crop cover in 2 km (in one model, $P = 0.257$). Cavity-nesting bee species richness was higher in sites with higher herbaceous plant richness (Fig. 2b), and in larger gardens (Fig. 2c), and was lower in sites with high mulch cover in 100- by 100-m plots (Fig. 2d). The best model predicting ground-nesting abundance included only garden size ($P = 0.031$), and abundance was higher in larger gardens (Fig. 3a). Ground-nesting bee richness was best predicted by the leaf litter cover in 1- by 1-m plots ($P = 0.015$), mulch cover in 100- by 100-m plots ($P = 0.038$), and by garden size ($P = 0.016$). Ground bee richness was lower in sites with more leaf

litter (Fig. 3b) and with more mulch (Fig. 3c), and was higher in larger gardens (Fig. 3d).

Small and large bee abundance did not significantly correlate with any local or landscape features, but medium bee abundance differed depending on changes in both local and landscape characteristics of gardens (Fig. 4). The top 10 models predicting small bee abundance were similar according to AICc values, and the averaged model included garden size (included in 3 of the top 10 models, $P = 0.078$), lawn cover in 100- by 100-m plots (in four models, $P = 0.108$), number of woody plants in 20- by 20-m plots (in two models, $P = 0.255$), number of flowers (in two models, $P = 0.291$), and the cover of concrete and buildings in 100- by 100-m plots (in two models, $P = 0.225$). No factors were significantly correlated with small bee abundance. The model for medium bee abundance included both local and landscape variables including grass cover in 1- by 1-m plots ($P = 0.018$), lawn cover in 100- by 100-m plots ($P = 0.004$), garden size ($P = 0.013$), and medium intensity developed land in 2 km ($P < 0.001$). Medium bee abundance was higher in sites with more grass cover in 1- by 1-m plots (Fig. 4a), with more lawn cover in 100- by 100-m plots (Fig. 4b), and in larger gardens (Fig. 4c), and was lower in sites with more medium intensity developed land in 2 km (Fig. 4d). The model explaining abundance of large bees only included garden size, but this was not a significant
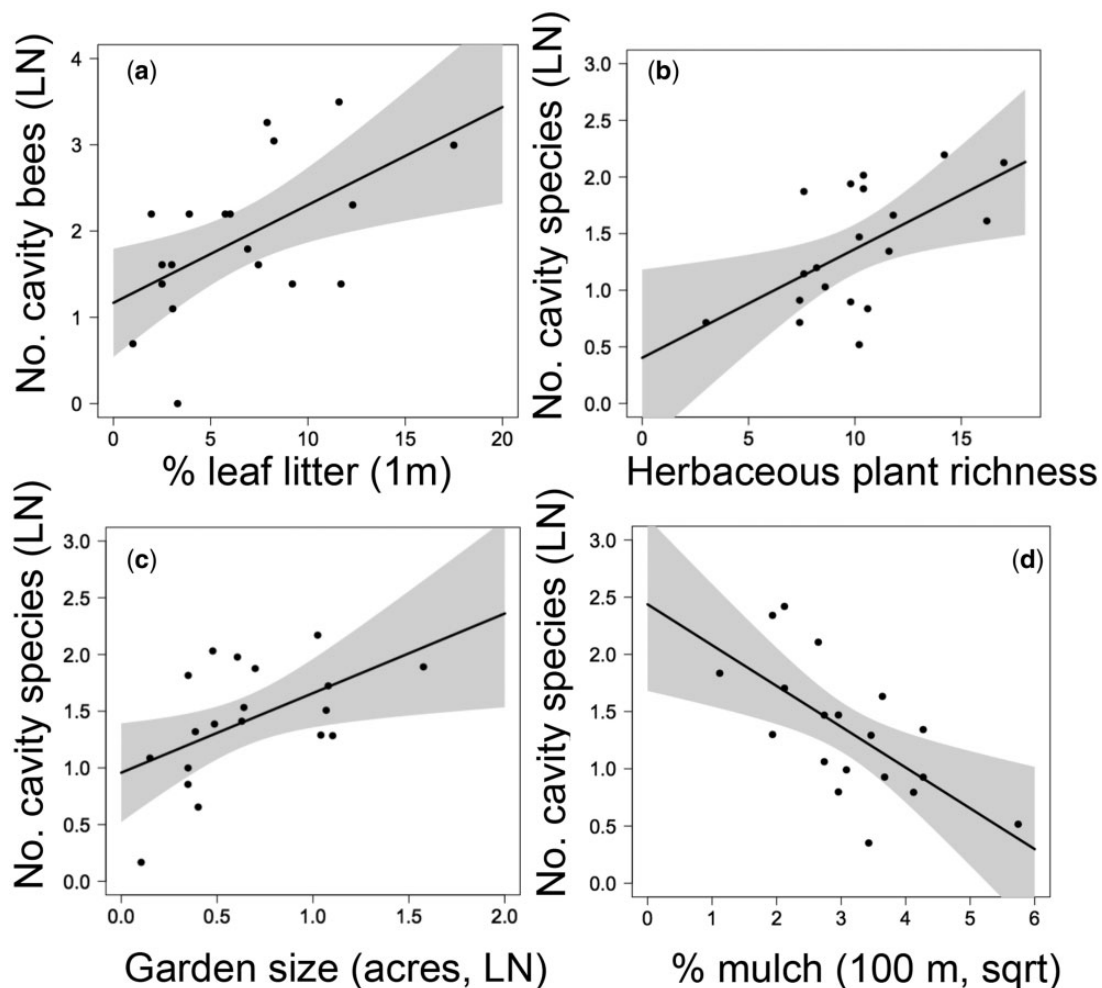

Fig. 2. Relationships between significant factors in generalized linear models and cavity-nesting bee abundance (**a**) and cavity-nesting bee species richness (**b–d**). All factors were significant at the $P < 0.05$ level. Each dot represents an urban garden study site, the lines show the best fit, and the grey area cover confidence bands based on the generalized linear models.

correlate of large bee abundance ($P = 0.064$). Thus, abundance of large bees did not correlate with any local or landscape characteristic.

Discussion

Our first research question addressed how many species of bees are found within urban gardens in the California central coast. We observed 55 bee morphospecies in central coast gardens, a number that is within the range of other studies that have examined bees in urban gardens. In California, specifically, others have documented 34 (Wojcik et al. 2008), 40 (Pawelek et al. 2009), and between 60–80 (Frankie et al. 2009) bee species in urban gardens. These studies all differ in terms of duration and numbers of gardens sampled with those at the lower end (e.g., 34 bees), representing a single garden sampled over many years, and those on the high end (e.g., 80 bees) from studies examining several gardens over several years. Other studies have documented between 54 and 66 species in New York City and Ohio urban gardens (Matteson et al. 2008, Pardee and Philpott 2014). Several studies have examined bees along a rural to urban gradient or in suburban (rather than urban) areas and have typically collected more bee species (58 to >110 bees), likely

because of the greater amount of open space or natural habitat in suburban and rural areas (Fetridge et al. 2008, Banaszak-Cibicka and Žmihorski 2011, Bates et al. 2011).

Our second question aimed to examine which local and landscape features of gardens correlate with abundance and species richness of bees in urban gardens, and to determine whether local or landscape factors are more important correlates of bee abundance and richness. Bee abundance and richness increased with garden size, and bee richness additionally increased with increases in floral abundance and decreases in mulch cover—all local scale factors. In other urban bee studies, declines in local resource availability negatively affect bees (Kearns and Oliveras 2009, Matteson and Langellotto 2010). For example, increases in nest site availability and increasing floral abundance and flower patch sizes (of either native or nonnative plants) positively correlate with bee abundance and richness (Gathmann and Tscharntke 2002, Frankie et al. 2005, Matteson and Langellotto 2010, Wojcik and McBride 2012, Pardee and Philpott 2014). Important to note in our study is that garden size was positively correlated with the amount of bare ground in 100- by 100-m plots, so any effects of increasing garden size may also be due to increases in the amount of bare ground—an important nesting resource for many bee species. We found that a decrease
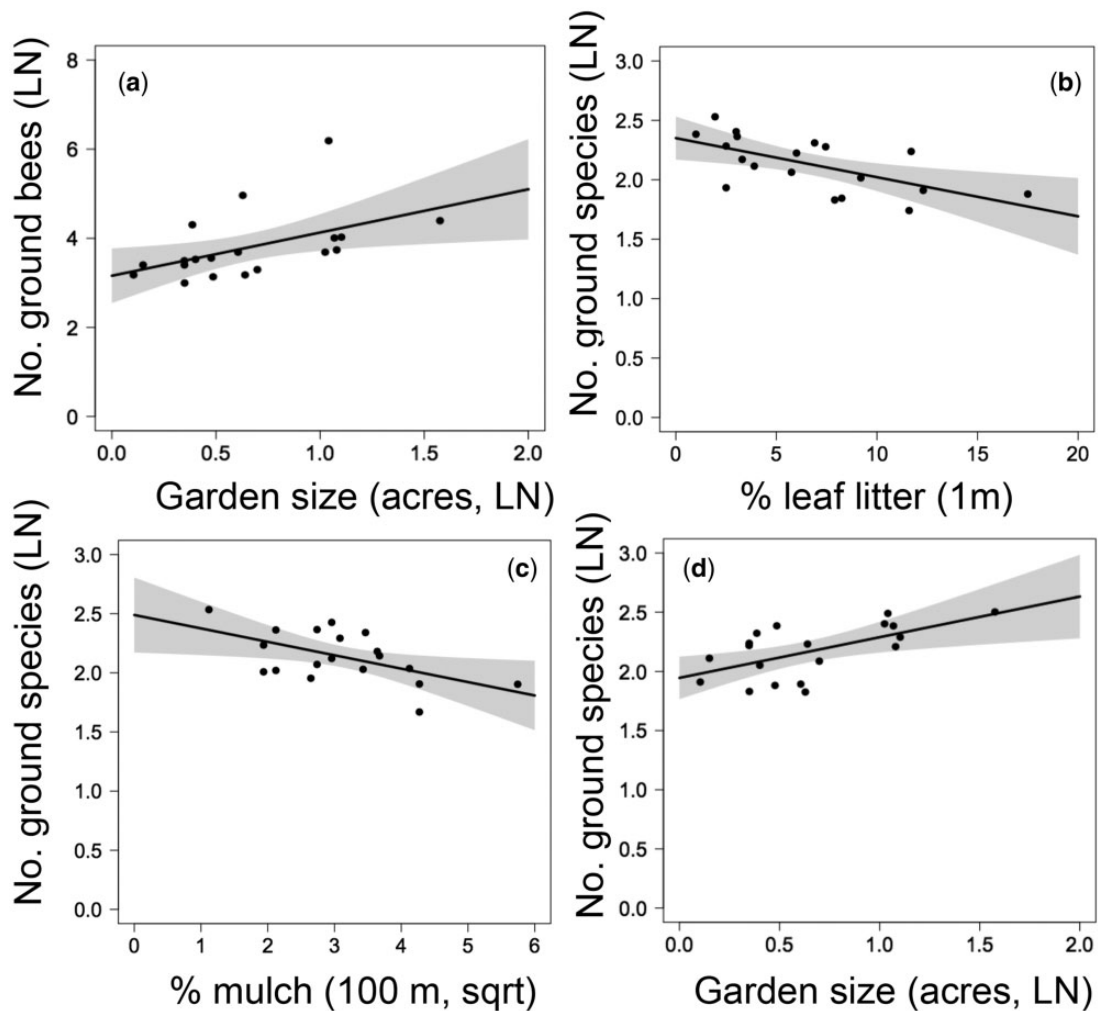

Fig. 3. Relationships between significant factors in generalized linear models and ground-nesting bee abundance (**a**) and ground-nesting bee species richness (**b–d**). All factors were significant at the $P < 0.05$ level. Each dot represents an urban garden study site, the lines show the best fit, and the grey area cover confidence bands based on the generalized linear models.
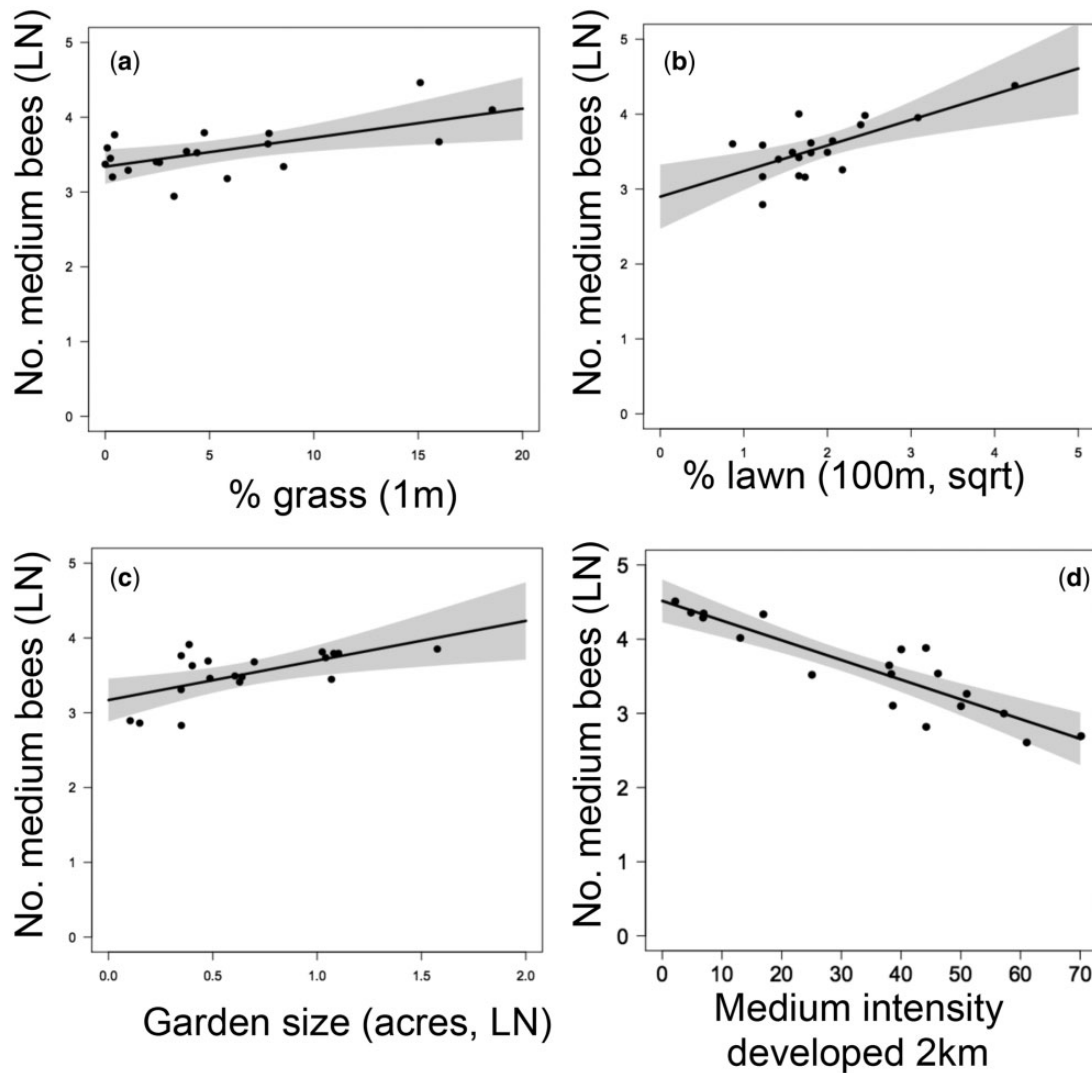
Fig. 4. Relationships between significant factors in generalized linear models and medium bee abundance (**a–d**). All factors were significant at the $P < 0.05$ level. Each dot represents an urban garden study site, the lines show the best fit, and the grey area cover confidence bands based on the generalized linear models.

in mulch cover (that may impede some ground-nesting bees) was positively associated with bee richness. Thus, our study corroborates previous work finding increases in floral abundance, increases in garden size (or increases in patch area), and increases in bare ground, with concomitant decreases in mulched area, all support bee abundance and richness. Typically, increases in urban or built structures within the landscape negatively affect bee abundance and richness (Hernandez et al. 2009, Bates et al. 2011, Hülsmann et al. 2015) and increases in amount of or nearness to open or natural habitat positively affect bee abundance and richness (Wojcik and McBride 2012, Pardee and Philpott 2014). We did find that landscape level factors influenced bee abundance or richness in our study, consistent with some earlier studies that have documented overwhelming impacts of local compared with landscape-scale factors on bee abundance and richness (e.g., Matteson and Langellotto 2010, Williams and Winfree 2013).

We also aimed to examine which local and landscape features of gardens correlate with abundance and species richness of ground- and cavity-nesting bees, and whether local or landscape predictors were more important. Several local factors correlated with changes in cavity-nesting and ground-nesting bee abundance and richness.

Cavity-nesting bee abundance and richness was high in sites with high leaf litter cover, high herbaceous plant richness, larger gardens, and low mulch cover (in 100- by 100-m plots). Cavity-nesting bees can nest in hollow twigs and branches, wood blocks, and crevices in man-made structures. Higher plant richness and higher leaf litter may be indicative of more abundant and diverse nesting resources for cavity-nesters. Larger gardens might support more food resources, and might also contain things like fences or other nesting resources for cavity-nesting bees. Such man-made nesting resources can promote cavity-nesting bee abundance and richness in urban areas (Cane et al. 2006). In our study gardens, wood-chip mulch is generally used in pathways and to cover weedy vegetation in the margins of gardens, and thus mulch cover might be indicative of lower plant density at a larger scale, which, in turn, might lower the availability of plant cavities. Several previous studies have found that cavity-nesting bees are more abundant in disturbed urban environments compared with nearly rural areas (Cane et al. 2006, Matteson et al. 2008, Hernandez et al. 2009). Similarly, local factors were the most important for predicting ground-nesting bee abundance and richness. Ground-nesting bee abundance and richness both were positively correlated with garden size, which in turn

positively correlated with bare ground in 100- by 100-m plots. In addition, ground-nesting bee richness increased in sites with low mulch cover and lower leaf litter cover. All of these factors point toward more access to bare ground, of course important for ground-nesting bees in urban areas (Frankie et al. 2009, Welzel 2011, Pardee and Philpott 2014). Thus, bee access to larger gardens, with more bare ground, may support conservation of ground-nesting bee biodiversity in urban gardens.

Finally, we aimed to examine which local and landscape features of gardens correlate with abundance and species richness of small, medium, and large bees, and whether local or landscape predictors were more important. Bee body size is indicative of flight distances in bees (Greenleaf et al. 2007), and so we would have expected for small bees to be more responsive to local factors, and medium and large bees to be more responsive to landscape-scale factors. To a limited extent, our results support these predictions. Medium sized bee abundance was predicted by both local and landscape factors, but we did not find any significant correlations with local or landscape factors for small or large bees. All of the factors included in the best predictive model for small bees were local factors (e.g., floral abundance, number of woody plants, lawn and concrete and building cover, and garden size), but none were significantly correlated with small bee abundance. Medium bee abundance increased in sites with more grass cover in 1- by 1-m plots, more lawn cover in 100- by 100-m plots, and in larger gardens, and also declined in sites with more medium intensity land cover in 2 km, a landscape factor. The positive response of medium bees to grass cover at both 1- by 1-m and 100- by 100-m scales was somewhat surprising. It may be that floral patches, such as within gardens, may stand out and encourage bee visitation when surrounded by grass areas with low floral abundance (Wojcik and McBride 2009). Notably, declines in medium intensity land also correspond to decreases in low intensity land, forest and grassland, and increases in high intensity land in 2 km. We did not detect any local or landscape correlates of large bee abundance. We only collected 146 large bees across the summer, compared with >800 medium bees, and >1,000 small bees. Both large numbers of small bees (from a very diverse taxonomic group of morphospecies) and the small numbers of large bees may have prevented us from detecting effects on these groups of bees due to species specific responses, or low sample sizes.

Interestingly, a large fraction (38.7%) of the medium bees collected were honey bees (*A. mellifera*), and thus the response of medium bees is likely large driven by the response of honey bees to local and landscape factors. Many studies describe *A. mellifera* to be very common in urban garden studies (e.g., Tommasi et al. 2004, Matteson et al. 2008, Frankie et al. 2009), and may thrive in urban green spaces as floral generalists (Threlfall et al. 2015). In another types of landscapes, *A. mellifera* responds strongly to landscape scale changes with increased density in less seminatural habitats, thus showing adaptation to more fragmented habitats and patchy resources (Steffan-Dewenter et al. 2002), such as in medium intensity developed areas.

In conclusion, both local and landscape characteristics contribute to maintaining bee communities in urban gardens by supporting potential nesting habitats outside the gardens and providing floral resources to bees within the gardens (Goddard et al. 2010, Frankie et al. 2005). Urban gardens support a high abundance and richness of bees, but bees of different body sizes and different nesting strategies responded to different suites of factors, often at different spatial scales. Of all dependent variables examined, almost all of the significant explanatory variables were local factors with only medium bees responding to one landscape factor. That bees, generally,

are responding to local, more so than landscape level changes, in urban areas is an important finding, given that gardeners can more easily manipulate factors at the local, rather than landscape scale. With increased garden size, more diverse herbaceous vegetation, higher floral abundance, and less use of mulch, people may be able to promote and conserve biodiversity of bees in urban gardens.

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