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Floral abundance, richness, and spatial distribution drive urban garden bee communities

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Abstract

In urban landscapes, gardens provide refuges for bee diversity, but conservation potential may depend on local and landscape features. Foraging and population persistence of bee species, as well as overall pollinator community structure, may be supported by the abundance, richness, and spatial distribution of floral resources. Floral resources strongly differ in urban gardens. Using hand netting and pan traps to survey bees, we examined whether abundance, richness, and spatial distribution of floral resources, as well as ground cover and garden landscape surroundings influence bee abundance, species richness, and diversity on the central coast of California. Differences in floral abundance and spatial distribution, as well as urban cover in the landscape, predicted different bee community variables. Abundance of all bees and of honeybees (*Apis mellifera*) was lower in sites with more urban land cover surrounding the gardens. Honeybee abundance was higher in sites with patchy floral resources, whereas bee species richness and bee diversity was higher in sites with more clustered floral resources. Surprisingly, bee species richness and bee diversity was lower in sites with very high floral abundance, possibly due to interactions with honeybees. Other studies have documented the importance of floral abundance and landscape surroundings for bees in urban gardens, but this study is the first to document that the spatial arrangement of flowers strongly predicts bee abundance and richness. Based on these findings, it is likely that garden managers may promote bee conservation by managing for floral connectivity and abundance within these ubiquitous urban habitats.

Keywords: Apidae, biodiversity conservation, connectivity, resource distribution, spatial ecology, urbanization

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Introduction

Bees are important contributors to pollination services, but are currently facing a range of threats. Many bee species currently face population declines stemming from several different processes, including a low, discontinuous supply of floral resources, disease, habitat fragmentation, and climate change (Potts *et al.*, 2010; Cameron *et al.*, 2011; Giannini *et al.*, 2012; Hung *et al.*, 2015; Scheper *et al.*, 2015). Bees and bee diversity benefit the pollination of crop and non-crop plants, thus it is critical to understand the factors that drive bee abundance and richness (Klein *et al.*, 2003; Breeze *et al.*, 2011; Winfree *et al.*, 2011). Habitat loss and change across landscapes can cause changes in plant reproductive success, although in some habitats or landscapes some of these effects may be mitigated through landscape management techniques (Harrison & Winfree, 2015).

Urban gardens can provide semi-natural habitat that may act as a refuge for biodiversity, including bees (Goddard *et al.*, 2010; Tanner *et al.*, 2014). The area in urban gardens often

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determines the amount of green space in many urbanized cities, and in some cities, urban gardens cover between 23 and 36% of the city area (Gaston *et al*., 2005; Loram *et al*., 2007; Mathieu *et al*., 2007; Cameron *et al*., 2012). Urban gardens support many local, landscape, and socio-political features that may conserve biodiversity. For instance, local features such as mulch cover and flowering plant species richness augment spider activity and richness (Otoshi *et al*., 2015). Garden size and socio-economic status of gardeners are crucial components for promoting avian richness and plant diversity (van Heezik *et al*., 2013). Further, urban gardens provide floral and nesting resources that may benefit insects (Wojcik *et al*., 2008). Individual gardens may strongly differ in management techniques and thus in vegetation and insect composition (Loram *et al*., 2007). For bees in particular, carefully planned garden designs, including floral abundance, plant species richness, and appropriate plot sizes can support bee diversity and bee habitat (Frankie *et al*., 2005; Samnegard *et al*., 2011; Baldock *et al*., 2015). Urban gardens are a key component of bee conservation because they can be managed for continuous floral resources (Threlfall *et al*., 2015). Currently, however, there is a dearth of information about how the specific features of garden design influence bee communities (Wojcik *et al*., 2008). There is also a lack of specific information about how the abundance of one common introduced species (*Apis mellifera*) is influenced by garden design, despite its ubiquity in human dominated landscapes, including urban landscapes in much of the world (e.g. Tommasi *et al*., 2004, Matteson *et al*., 2008, Frankie *et al*., 2009).

Understanding the diversity and distribution of flowers, an important bee resource, may contribute to understanding bee communities and conservation in urban landscapes. In general, understanding spatial connectivity can help predict species distribution, species persistence and migration (Moilanen & Nieminen, 2002). Further, the spatial distribution of resources (e.g. clustering, size, patchiness) influence animal foraging behaviour, species richness, and species composition (Goulson, 1999; Ribas *et al*., 2005; Braaker *et al*., 2014). For bees specifically, diversity, abundance, composition, and spatial distribution of floral resources affect bee foraging behaviour, abundance, species richness, and community composition and thus may strongly affect interactions between pollinators and plants (Torné-Noguera *et al*., 2014; Harrison & Winfree, 2015). At very local scales, bee visitation rates to flowers can differ with floral resource patch size (Sih & Baltus, 1987) or with the presence of other plant species in the same habitat patch (Thomson, 1981). At larger spatial scales, visitation rates to flowers may be influenced by floral connectivity in a landscape (Torné-Noguera *et al*., 2014). Patchy (Hines & Hendrix, 2005), and heterogeneous spatial resources across a landscape may allow foraging bees to switch to different floral resources and increase offspring production (Williams & Kremen, 2007). Yet, in some circumstances, floral diversity, rather than floral density drives bee foraging and as such, understanding the specific factors that drive bee population and diversity are important to increase pollination services (Jha & Kremen, 2012).

In this study, we examined floral resources and bee communities in urban gardens to determine how floral abundance, floral diversity, and floral spatial distributions within urban gardens are associated with changes in bee richness and abundance. Specifically, we tested the responses of the bee community to changes in floral resources with four response variables: abundance of all bees (hereafter bee abundance), abundance of *Apis mellifera* (hereafter *A. mellifera* abundance), species richness of all bee species (hereafter bee species richness), and diversity of all bee species (hereafter bee diversity). We investigated two main research questions: (1) Does floral abundance and diversity in gardens correlate with bee abundance, *A. mellifera* abundance, bee species richness, and bee diversity? (2) Does the spatial distribution or connectivity of floral resources within gardens influence bee abundance, *A. mellifera* abundance, bee species richness, and bee diversity? We hypothesized that increases in floral abundance and diversity and more clustered floral resources would result in increases in bee abundance, *A. mellifera* abundance, bee species richness, and bee diversity in urban gardens. We also examined the role of floral abundance and spatial distribution in relation to other local and landscape characteristics of urban gardens important for urban bee communities.

Methods

Study sites

Between July and early August 2015 we surveyed 18 urban gardens, ranging in size from 444 to 15,525 m^2, across three counties (Monterey, Santa Clara, and Santa Cruz) in the California central coast (fig. 1). All gardens included vegetable patches that had been in regular cultivation for at least 5 years, and many also included various ornamental, native, and non-native plants. In the centre of each garden, we established a 20 × 20 m^2 plot within which all sampling was performed.

Bee surveys

We sampled bees with elevated pan traps and hand netting (Grundel *et al*., 2011). We constructed pan traps using 400 ml plastic bowls (yellow, white, and blue) painted with Clear Neon Brand and Clear UV spray paint. We placed pan traps over 3 days in early July, from approximately 8 AM until 7 PM on each day, and trapped bees were collected daily. We placed three 1 m tall polyvinyl chloride (PVC) pipes in the ground in a triangle formation, 5 m apart within each of the 20 × 20 m^2 plots, and placed one bowl of each colour on top of PVC tubes (Tuell & Isaacs, 2009). We filled bowls with 300 ml of water and 4 ml of unscented Dawn dish soap. In addition, we sampled bees using aerial nets at each site, over the days of 7–9 July, 31 July, and 2 August 2015. We searched for and captured bees in nets for a total of 30 min per site. We netted bees that were observed on flowers, within 20 m of and inside the 20 × 20 m^2 plots in each site. We stored all captured bees for later identification. We performed bee identifications with reference to online resources, image databases, books, and dichotomous keys (Roberts, 1973*a*, *b*; Michener, 2007; Gibbs, 2010; Frankie *et al*., 2014; Ascher & Pickering, 2015; Packer, 2015). We identified all specimens to the highest taxonomic level possible, and for more difficult specimens we allocated them to morphospecies. We also compared our specimens to specimens held in the Kenneth S. Norris Center for Natural History on the University of California, Santa Cruz campus. All voucher specimens are housed in the Philpott Laboratory at the University of California, Santa Cruz.

Floral surveys

For floral surveys, we divided the 20 × 20 m^2 plot into 100 2 × 2 m^2 quadrats and assigned each quadrat a spatial

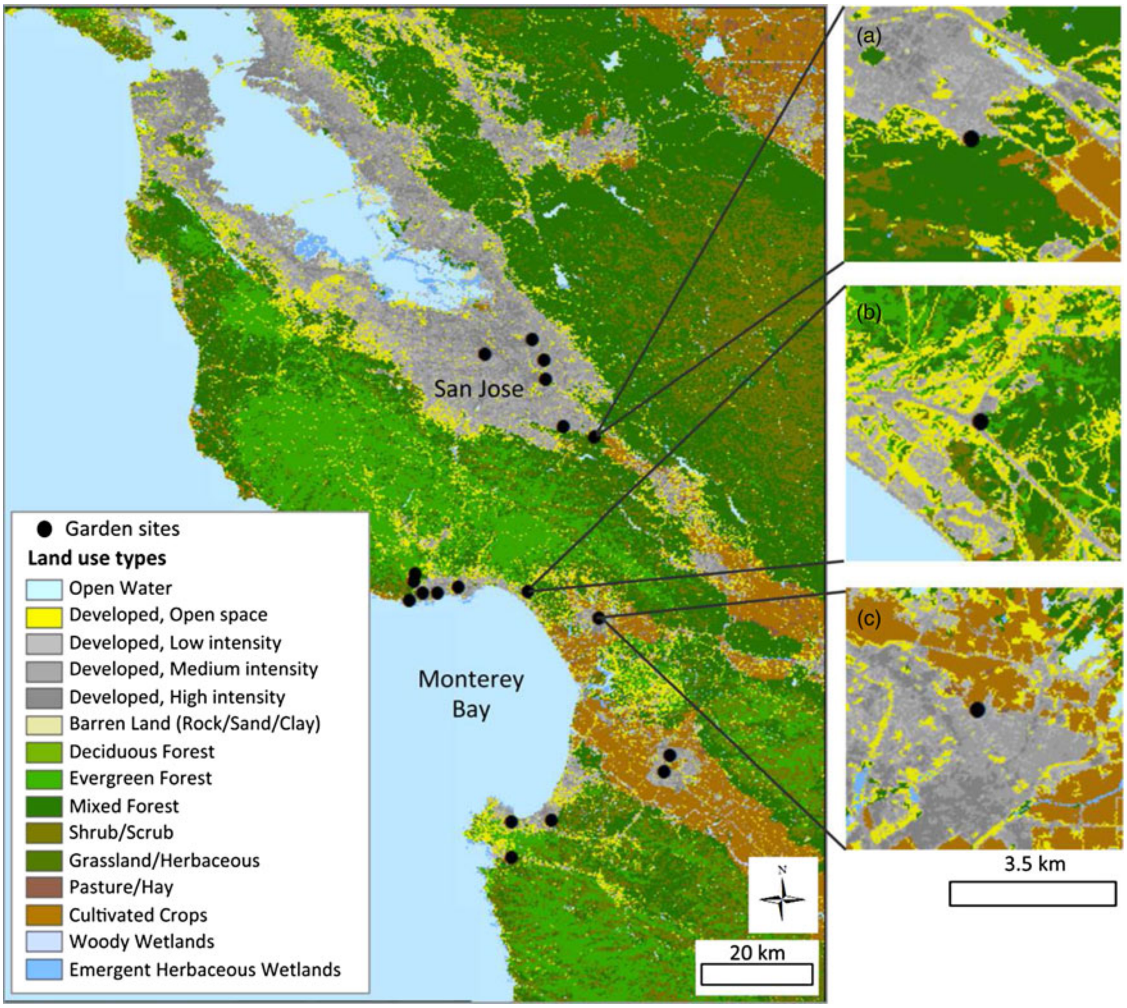

Fig. 1. A map of the Central coast region of California showing the 18 urban garden sites in Monterey, Santa Clara, and Santa Cruz Counties, and land cover types in the study region and surrounding the garden study sites with three zoomed in panels to show (a) a garden surrounded primarily by urban and natural land, (b) a garden surrounded by natural, open, and urban land, and (c) a garden surrounded by primarily urban and agricultural land.

coordinate (A-J, 1–10) for use in spatial analysis. Before counting flowers, we spent 30–45 min observing bees and noting all floral species being visited by bees in that site on that day. Then, in each quadrat, we counted or estimated floral abundance of species being visited by bees. Most flowers were exhaustively counted. For flower species where we estimated abundance, we counted the number of flowers on each of three inflorescences, took the average value, and then multiplied by the total number of inflorescences in the quadrat. We noted the colours of each flower (white, yellow, purple, red, orange, purple, or blue) and identified all flowering plants to species or morphospecies.

Site characteristics

To determine if local- and landscape-scale characteristics had an effect on bee species richness and abundance, we measured ground cover within our plots, and classified nearby land cover types surrounding each site. At the local scale, we noted the percent ground covered with bare soil, herbaceous plants, and mulch within four 1×1 m^2 plots in our 20×20 m^2 plot. At the landscape scale, we classified the land cover types within 2 km buffers surrounding each garden with data from the 2011 National Land Cover Database (NLCD, 30 m resolution) (Homer *et al.*, 2015). We chose 2 km buffers as 1.5–2 km is the median maximum foraging range of bee species for which data exist (Zurbuchen *et al.*, 2010). We created four surrounding landscape categories: natural habitat, open, urban, and agriculture by combining NLCD land cover classes. Our natural habitat area included deciduous (NLCD number 41), evergreen (42), and mixed forests (43), dwarf scrub (51), shrub/scrub (52), and grassland/herbaceous (71) and is the only landscape category with predominantly natural vegetation. Three of these categories (urban, open and agriculture) represent areas heavily impacted by humans, although they differ in the predominant ground cover. According to the NLCD descriptions (see Homer *et al.*, 2015), urban areas (combining low [22], medium [23], and high-intensity developed land [24]) contain between 20 and 100% impervious surface; open areas (21) are vegetated mostly in the form of lawn grass; and agricultural areas (combining pasture/hay [81] and cultivated crops [82]) have at least 20% crop or pasture grass cover. We chose these four landscape categories based on knowledge of bee foraging and nesting needs from the literature. Other land cover types covered <5% of the total area and were not included. We assessed land cover with spatial statistics tools in ArcGIS v. 10.1.

Data analysis

To answer our two questions, we used four different response variables: bee abundance, *A. mellifera* abundance, bee species richness, and bee diversity. Bee diversity was calculated with the Shannon–Wiener index (H´). We pooled all pan trap and hand-netting data from each site for all analysis. We included floral abundance characteristics, floral distribution characteristics, other local factors, and landscape factors as explanatory variables in a single statistical model (see below). Floral characteristics included total number of flowers and flower species per site, mean number of flowers per quadrat, max number of flowers per quadrat, mean number of white flowers per quadrat, as well as the spatial distribution of flowers. Aside from floral resource distribution, all local and landscape factors included are known to affect bee species richness and abundance in our study sites (Quistberg *et al.*, 2016). To our knowledge, no study to date has looked at floral resource distribution as an additional predictor of bee communities in urban gardens. We found a large range in all measured variables in the different study sites (Supplementary Table 1). To calculate the spatial distribution of flowers, we mapped the 100 quadrats for each site and joined the floral resource data to each quadrat in ArcGIS 10.1. Then for each site, we used spatial statistics tools to calculate six nearest-neighbour ratios (NNRs) for each site based on data for quadrats with ≥15, ≥50, and ≥100 flowers, ≥15 white flowers, and ≥2 species of flowers. We chose floral abundance thresholds of 15, 50, and 100 flowers per quadrat because those corresponded to roughly 40, 20, and 10% of all quadrats sampled. We included quadrats with white flowers given their importance for urban bees in our sites (Quistberg *et al.*, 2016). NNR calculates spatial patterns, such as clustering and dispersion. A smaller NNR value indicates a higher degree of clustering. Thus our analysis included five floral abundance variables (total floral abundance in a site, total floral species richness in a site, the mean number of flowers per quadrat, mean number of white flowers per quadrat, and the max number of flowers per quadrat), five floral distribution variables (site-level NNR values for quadrats with ≥15, ≥50, or ≥100 flowers, ≥15 white flowers per quadrat, and ≥2 species of flowers per quadrat), three other local factors (percent ground cover with bare ground, herbaceous vegetation, and mulch), and four landscape variables (percent of landscape with open, natural, agricultural, or urban land use within 2 km) for 18 explanatory variables.

To check for correlation among explanatory variables, we ran Pearson's correlations. We divided explanatory variables into four groups: (1) floral abundance and richness, (2) floral spatial distribution, (3) other local factors, and (4) landscape factors, examined which variables were highly correlated ($P < 0.01$), and selected one of the correlated variables as a representative for subsequent analysis (see Supplementary Methods). The nine explanatory variables chosen for subsequent analyses were mean number of flowers per quadrat, total flower species richness, NNR for quadrats with ≥15 flowers, NNR for quadrats with ≥50 flowers, NNR for quadrats with ≥100 flowers, mulch cover, herbaceous cover, urban land cover in 2 km, and agriculture in 2 km.

We used generalized linear models (GLMs) with the glm function in R (R Development Core Team, 2014) to examine relationships between selected floral abundance and distribution variables, other local factors, landscape characteristics and bee abundance, *A. mellifera* abundance, bee species richness, and bee diversity. We tested all combinations of different variables with the 'glmulti' package (Calcagno & de Mazancourt, 2010) and selected the top model based on the AICc values. For models where the AICc for top models was within 2 points of the next best model, we averaged models (up to the top ten models) with the MuMIn package (Barton, 2012) and report conditional averages for significant model factors. As dependent variables were normally distributed, we used Gaussian error structure for GLMs (i.e. models were equivalent to multiple linear regression models), and report corrected Akaike Information criterion (AICc) values, *P*-values, and multiple linear model R^2 values for all best models. All residuals from the best models conformed to the conditions of normality as checked with QQ-Plots and Shapiro–Wilk tests.

Because of the potential for managed hives of *A. mellifera* to influence bee abundances, we compared bee abundance, *A. mellifera* abundance, bee species richness, and bee diversity in sites with and without known managed honeybee hives with *t* tests. Finally, we examined correlations between *A. mellifera* abundance and bee species richness and bee diversity with simple linear regressions.

Results

We collected 1354 bee individuals from 43 species. We collected 5 bee families; the most abundant family was Apidae representing 70% of total individuals captured. The most abundant bee species was *A. mellifera* (58% of individuals captured), followed by *Halictus tripartitus* (10.1%), *Bombus caliginosus* (4.4%), and *Bombus vosnesenskii* (1.5%).

Bee abundance, *A. mellifera* abundance, bee species richness, and bee diversity were most affected by urban land cover, floral abundance, and floral spatial distribution. The model that best explained bee abundance included only urban land cover within 2 km (table 1). Increasing urban land cover predicted lower bee abundance ($P = 0.015$, fig. 2a). The model that best explained *A. mellifera* abundance included urban land cover and NNR for quadrats with ≥15 flowers (table 1). *A. mellifera* abundance decreased with higher urban cover ($P < 0.001$, fig. 2b) and increased as floral resources became more patchy ($P < 0.001$, fig. 2c). The models that best explained bee species richness and bee diversity both included mean number of flowers in a quadrat and NNR for quadrats with ≥15 flowers (table 1). Bee species richness declined as floral abundance increased ($P = 0.018$, fig. 3a) and as floral resources became more patchy ($P = 0.031$, fig. 3b). Likewise, bee diversity declined as floral abundance increased ($P = 0.014$, fig. 3c), and as floral resources became more patchy ($P = 0.003$, fig. 3d). We also noted negative correlations between the abundance of *A. mellifera* and bee species richness ($R^2 = -0.561$, $P < 0.05$, fig. 4a) and bee diversity ($R^2 = -0.715$, $P < 0.01$, fig. 4b).

Table 1. GLM results table showing all response variables, explanatory variables included in the best models, AICc values, residual degrees of freedom, and R^2 values for general linear models.

Response variable	Explanatory variables included in best model	AICc for best model	df	R^2
Bee abundance	Urban land cover within 2 km	175.72	16	0.312
Apis mellifera abundance	Urban land cover within 2 km, NNR for quadrats with ≥15 flowers	149.48	15	0.753
Bee species richness	Mean number of flowers per quadrat, NNR for quadrats with ≥15 flowers	94.69	15	0.508
Bee diversity (H′)	Mean number flowers, NNR for quadrats with ≥15 flowers	25.95	15	0.619

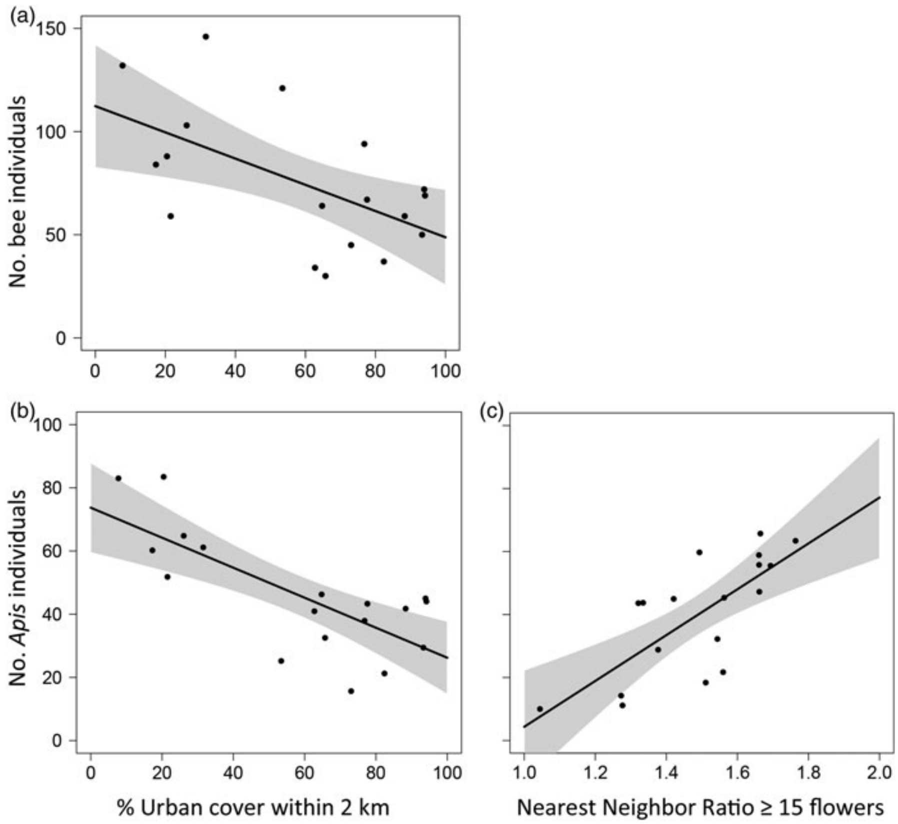

Fig. 2. Correlations showing relationships between percent urban land cover and (a) number of bee individuals and (b) number of *Apis mellifera* individuals and the nearest-neighbour ratio (NNR) for quadrats with ≥15 flowers and (c) number of *A. mellifera* for bees collected in urban gardens in the Central coast region of California. The lines show the best fit and the grey area cover confidence bands based on the generalized linear models. Smaller NNR values indicate stronger floral clustering.

Discussion

We investigated the effect of floral abundance, distribution, and other local and landscape factors on bee communities and found that floral spatial distribution is one of the most important drivers of bee species richness, bee diversity, and *A. mellifera* abundance. In addition, floral abundance and urban land cover are important drivers of bee communities. Bee abundance was significantly negatively correlated with urban cover in the landscape, but not with other floral abundance or distribution factors, or ground cover characteristics. Habitat loss associated with urbanization is one main cause of bee declines (Martins *et al.*, 2013), and other studies have documented drops in bee abundance with increases in concrete, buildings, and other types of impervious cover at the landscape level (Bates *et al.*, 2011; Threlfall *et al.*, 2015). In addition, impervious surfaces limit nesting opportunities for bees and can increase bee foraging distances (Fortel *et al.*, 2014). In our study, natural and open land cover negatively correlated with urban land cover, thus these variables, which were excluded from the analysis, may also impact bee abundance positively. Therefore, declines in urban developed cover and increases in cover by natural habitats (e.g. forest and grassland) likely both promote bee abundance, especially in areas with little natural habitat remaining (Winfree *et al.*, 2009). For example, natural habitat provided by green roofs or small patches of ornamental plants can provide suitable habitat for bees to forage and collect floral resources (Tonietto *et al.*, 2011; Garbuzov *et al.*, 2015).

We found that the abundance of *A. mellifera*, by far the most common bee species collected in our study, declined with

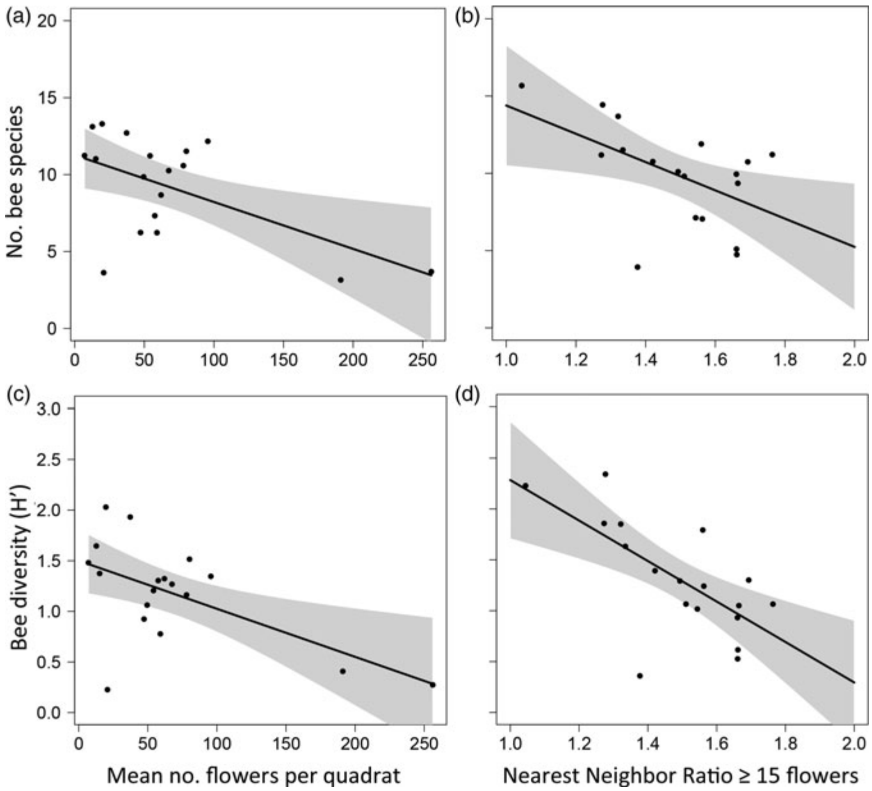

Fig. 3. Correlations showing relationships between mean number of flowers per 2 × 2 m^2 quadrat and (a) bee species richness and (c) bee diversity, and between the nearest-neighbour ratio (NNR) for quadrats with ≥15 flowers and (b) bee species richness and (d) bee diversity for bees collected in urban gardens in the Central coast region of California. The lines show the best fit and the grey area covers confidence bands based on the generalized linear models. Smaller NNR values indicate stronger floral clustering.

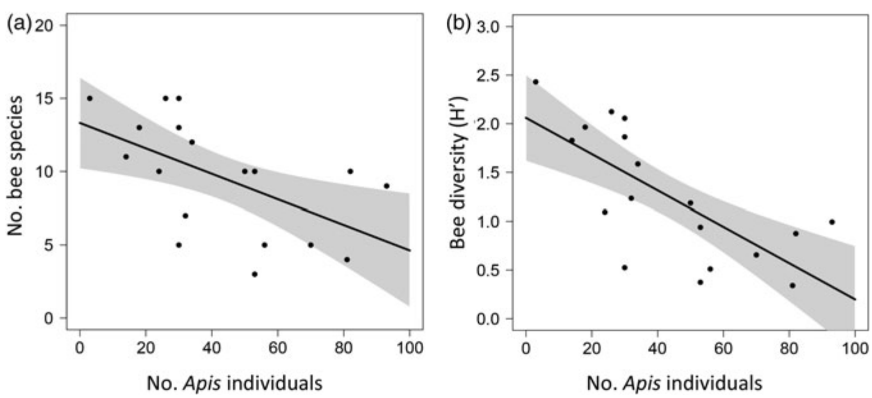

Fig. 4. Correlations showing relationships between the number of honeybees (*Apis mellifera*) and (a) bee species richness and (b) bee diversity for bees collected in urban gardens in the Central coast region of California. The lines show the best fit and the grey area covers confidence bands based on the generalized linear models.

increases in urban cover, increased with more dispersed floral resources, but did not respond to other local factors. Increasing amount of urban cover is implicated in declines of bee abundance, generally (e.g. Potts *et al.*, 2010). However, *A. mellifera* usually thrives in urban green spaces such as public parks and residential neighbourhoods, more so than other wild bees. This is likely because *A. mellifera* is a floral generalist, because wild bees may lack appropriate nesting habitat in urban areas (Threlfall *et al.*, 2015), and because honeybees are most likely managed and nests are provided for them. Although many studies note *A. mellifera* as the most common bee found in urban garden studies (e.g. Tommasi *et al.*, 2004; Matteson *et al.*, 2008; Frankie *et al.*, 2009), none actually examine whether landscape features correlate with *A. mellifera* abundance within urban habitats. In addition, few studies have described floral spatial distribution as an important predictor for honeybees. We found that *A. mellifera* abundance was higher in sites with more patchy (i.e. less clustered) floral resources and this finding may provide insight for managing *A. mellifera* abundance in urban gardens. *A. mellifera* is a generalist species and its medium size permits it to forage large distances (Greenleaf *et al.*, 2007), thus it is unlikely that *A. mellifera* abundance would be negatively affected by dispersed floral resources (Beekman & Ratnieks, 2000). In other landscapes, *A. mellifera* abundances were positively associated with large landscape scales in landscapes with fewer semi-natural habitats, thus showing adaptation to more fragmented habitats and patchy resources (Steffan-Dewenter *et al.*, 2002). Eusocial insects, such as *A. mellifera*, that live in large colonies recruit foragers to search for patches with abundant resources. One study reported the colony health or 'energy status' of *A. mellifera* influenced the foraging distance, for instance, when the floral resources were high *A. mellifera* foraged small patches and short distances, and when resources were low they foraged longer distances and larger patches (Schneider & McNally, 1993). Therefore, *A. mellifera* may be better equipped than other bees to experience spatial changes in floral resources because they forage at variable distances when floral resources are also variable. Finally, many urban sites, including gardens, may actively promote *A. mellifera* by maintaining managed hives. Of our 18 sites, four had managed hives at the time of our study, but we do not know if homeowners in private property surrounding other sites may have had hives. *A. mellifera* abundance was significantly higher (*t* test, $P = 0.006$) in the four sites with known managed hives, but there were no differences in bee species richness, bee diversity, or (non-*A. mellifera*) bee abundance (*t* tests, $P > 0.05$) in sites with and without known managed hives.

We found that changes in bee species richness and bee diversity were largely driven by floral abundance (but not landscape factors). While floral abundance is often associated with higher bee richness in urban areas (e.g. Matteson & Langellotto, 2010; Wojcik and McBride, 2012; Hülsmann *et al.*, 2015), we found that bee species richness and diversity was lower in sites with more flowers and patchier flower resources. This may be due to sampling effects whereby more flowers available result in fewer bees captured in pan traps. Our analysis examined mean number of flowers per quadrat, but this was also correlated with total floral abundance, maximum floral abundance per quadrat, and also with floral abundance of white flowers, so any of these variables may drive the observed effects.

In contrast to patterns for *A. mellifera* abundance, we found that sites with more clustered floral resources supported higher bee richness and bee diversity. This is a novel finding as the first study to assess how floral distribution within urban ecosystems impacts bee communities and potentially bee conservation. Others have documented increases in abundance of individual bee groups (e.g. bumble bees) in areas with patchy floral resources (Wojcik & McBride, 2012), but have not examined entire communities. Clustered floral resources may support an array of bees that forage both short and long distances, but may be particularly important for smaller bees that exhibit limited foraging ranges (Zurbuchen *et al.*, 2010). Further, different bees (even within the same genus) may respond differently to floral patch size (Sowig, 1989). The frequency of pollinator visits may decrease as flower patch size increases because searching for unvisited flowers in small patches may allow bees to optimize their foraging strategy (Goulson, 2000). Similarly, floral density effects are strong at low densities because plants facilitate one another's pollinator attraction, while higher floral densities tend to have weak pollinator attraction because plants compete for pollinator attraction (Essenberg, 2012). Bee conservation in intensified agricultural systems (with low floral resources) can be bolstered by adding clumped spatial elements such as hedgerows or buffer strips (Klein *et al.*, 2007). These additions likely work to augment bee diversity because bees in human-managed systems respond to clustered floral resources. For example, in a different agricultural system (tropical coffee systems), bee diversity did not respond to floral resources clumping at the field scale, but bee diversity increased in sites with branch and shrub scale floral clustering, thus emphasizing the notion that responses of bee diversity to floral clustering are dependent both on floral abundance but also on spatial scale (Veddeler *et al.*, 2006).

One of the striking patterns found is that *A. mellifera* abundance and bee species richness and bee diversity responded to floral spatial distribution in opposite ways – with bee species richness responding positively to clustering, and *A. mellifera* abundance responding negatively to floral clustering. This prompts the question of whether interactions between *A. mellifera* and other bee species may be driving observed patterns. We posit that due to extensive foraging ranges and generalist preferences, *A. mellifera* could be foraging in dispersed floral patches, allowing smaller bees or other bee species to occupy the clustered patches of flowers. *A. mellifera* presence may restrict access by other bees through interference competition, or by apparent competition if *A. mellifera* deplete nectar resources driving other bees to search elsewhere (e.g. Schweiger *et al.*, 2010). Yet, there may be minimal interference of floral resources by honeybees compared to native bees because different bee groups may not share floral resources (Pedro & Camargo, 1991). The assumed widespread effects of *A. mellifera* on other bees are often based on observations, but not long-term population assessments (Paini, 2004); thus, careful consideration is necessary. Some studies have taken an experimental approach to examine the influences of removal of one numerically dominant bee on foraging patterns of other species. For example, removal of a numerically dominant bee (*Bombus* sp.) from alpine meadows in Colorado influenced the floral visitation of other pollinator species (Brosi & Briggs, 2013). One experimental study demonstrated that in small and isolated flower patches, increased honeybee density reduced visitation rates, niche breadth, and reproduction of the red mason bee (Hudewenz & Klein, 2015). Another potential mechanism driving negative relationships between honeybees and other bees may be the transmission of disease from *A. mellifera* to wild bees (Furst *et al.*, 2014). Regardless, any interactions between *A. mellifer*a and other bee species may have important implications for pollination services in urban gardens (Greenleaf & Kremen, 2006). *A. mellifera* thrives in urban settings (Tommasi *et al.*, 2004), but their high floral visitations have led to a reduction in the fitness of native bees and the flowers other bees pollinate (Gross & Mackay, 1998). For some plant species, honeybees have poor pollination efficiency and may create discrepancies between higher bee visitation rates and lower seed sets in urban sites (Leong *et al.*, 2014). Certainly, further research and experimentation in understanding interactions between native bees and *A. mellifera* is warranted.

Urban gardens are important in bringing environmental awareness about ecosystem services to human communities and for sustaining biodiversity of ecological communities (Goddard *et al.*, 2010). Urban gardens connect fragmented areas impacted by urbanization and intensified agriculture by linking floral communities, bee communities, and stewardship by the gardeners. Increasing urbanization and habitat loss puts significant pressures on these isolated gardens to support great diversity, thus it is crucial to study how to diversify urban systems to promote biodiversity (Philpott *et al.*, 2014). Our main findings show that abundance and spatial distribution of floral resources and landscape factors are important for maintaining diverse and abundant bee communities and could contribute to management decisions within urban gardens. Our results suggest that bee diversity responded positively to spatial aggregations of floral resources, and that spatial arrangement of flowers is important in managing urban habitats for bees. Thus, gardeners might strive to plant several smaller clumped flower patches. At larger scales, promoting natural and open space within urban areas may also encourage overall bee abundance, richness, and conservation and pollination services within urban landscapes.

Supplementary material

The supplementary material for this article can be found at https://doi.org/10.1017/S0007485317000153

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