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5 **Influences of floral abundance, richness, and spatial distribution on urban garden bee**  
6 **communities**

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21

22 **Abstract**

23 Resource distribution strongly shapes ecological communities. For bees, spatial distribution of  
24 floral resources may influence foraging efficiency and population persistence, and thus pollinator  
25 communities and conservation. In urban landscapes, gardens provide refuges for bee  
26 biodiversity, and depending on local and landscape features, such as the distribution of floral  
27 resources, urban gardens may be managed to support bee conservation. We examined whether  
28 the abundance, richness, spatial distribution of floral resources within urban gardens influence  
29 bee abundance (overall and for common species), species richness, and diversity. We sampled  
30 bees using aerial surveys and pan traps, and assessed floral abundance and spatial patterns within  
31 19 urban gardens in the California central coast. We included other local and landscape variables  
32 that influence urban bees as additional explanatory factors. We found that floral abundance and  
33 spatial distribution, as well as landscape surroundings of the gardens all correlate with different  
34 components of bee communities in urban gardens. Bee abundance and honeybee (*Apis mellifera*)  
35 abundance negatively correlated with urban land cover surrounding the gardens. Honeybee  
36 abundance increased in sites with less clustered floral resources, whereas bee species richness  
37 and bee diversity increased in sites with more clustered floral resources. Surprisingly, bee species  
38 richness and diversity decreased in sites with very high floral abundance, potentially due to  
39 interactions with honeybees. Others have documented the importance of floral abundance and  
40 landscape surroundings for bees in urban gardens, but this study is the first to document that the  
41 spatial arrangement of flowers strongly predicts bee abundance and richness. Based on these  
42 findings, it is likely that garden managers may promote bee conservation by managing for floral  
43 connectivity and abundance within these ubiquitous urban habitats.

44

45 **Keywords:** Apidae, biodiversity, conservation, California, connectivity, resource distribution,  
46 spatial ecology, urbanization

47

## 48 **Introduction**

49         Spatial ecology examines how organisms persist in and respond to various landscape  
50 structures, patterns, fragmented habitats, and the distribution of resources across those  
51 landscapes (Hunter 2002). Metrics such as spatial connectivity help measure species distribution,  
52 species persistence and migration (Moilanen and Nieminen 2002), but also allow us to examine  
53 the foraging strategies that impact the variation in species community composition (Goulson  
54 1999, Braaker et al. 2014). The spatial distribution of resources (e.g. clustering, size, patchiness)  
55 directly influences animal foraging behavior, species richness, and species composition (Goulson  
56 1999, Ribas et al. 2005; Braaker et al. 2014). For instance, insect foraging behavior is influenced  
57 by the amount and diversity of available resources, as well as spatial relationships to other  
58 resources (Goulson 1999). Thus, the spatial distribution of resources and the diversity and  
59 abundance of resources is crucial in supporting an array of communities (Fridley 2002, Anderson  
60 et al. 2004, Jha and Kremen 2012). Further, spatial heterogeneity of resources is needed to  
61 maintain species composition and richness because it creates various niches that are exploited  
62 (Tilman and Pacala 1993). The importance of identifying spatial patterns associated with  
63 resource distribution is crucial in understanding area-restricted foraging behavior and to build  
64 models that heighten our understanding of community assembly (Pleasants and Zimmerman  
65 1979).

66         Bees are in decline globally due to low, discontinuous supply of floral resources, disease,  
67 habitat fragmentation, and climate change (Cameron et al. 2011, Giannini et al. 2012, Hung et al.

68 2015, Scheper et al. 2015). Because bees provide pollination services, it is critical to understand  
69 factors that drive bee abundance and richness (Breeze et al. 2011, Winfree et al. 2011). Bee  
70 communities respond to floral resources, and diversity of floral resources in a habitat and the  
71 spatial arrangement of floral resources can affect bee foraging behavior, abundance, species  
72 richness, and community composition of bees that visit a site (Harrison and Winfree 2015,  
73 Torné-Noguera et al. 2015). For example, bee visitation rates to *Nepeta cataria* in edges of  
74 wooded area differ between large and small patches of floral resources (Sih and Baltus 1987).  
75 Similarly, visitation rates to *Potentilla gracilis* are influenced by the presence of other plant  
76 species in the same habitat patch (Thomson 1981). Generally, small bees with limited foraging  
77 radius are easily influenced by floral connectivity in a landscape (Torné-Noguera et al. 2015).  
78 Resource distributions and connectivity within mosaic landscapes allow foraging orchard bees  
79 (*Osmia lignaria*) to switch to different floral resources and increase offspring production  
80 (Williams and Kremen 2007). Tallgrass prairie patches provide abundant floral resources and  
81 nesting sites at a spatial scale important for maintaining diversity and abundance of larger bees,  
82 such as bumblebees (Hines and Hendrix 2005). Yet, in some circumstances, floral diversity,  
83 rather than floral density drives bee foraging and as such, efforts to construct human-made  
84 landscapes through a bee lens may allow us to increase pollination services (Jha and Kremen  
85 2012). In any case, loss and changes to habitat causes changes in flower visitation and  
86 pollination success (Harrison and Winfree 2015). Thus, impacts of floral composition relative to  
87 space and time create complex interactions between pollinators and plants.

88         Urban gardens can provide habitat refuges for biodiversity, are heavily used by bees, and  
89 may support very patchy floral resources. Urban gardens provide semi-natural habitat that can be  
90 used by both humans and biodiversity (Goddard et al. 2010, Tanner et al. 2014). The abundance

91 of urban gardens determines the amount of green space in many urbanized cities, and the amount  
92 of urban green space varies from city to city (Cameron et al. 2012). For instance, in cities in  
93 England and New Zealand, urban gardens cover between 23-36% of the city area (Gaston et al.  
94 2005, Loram et al. 2007, Mathieu et al. 2007). Urban gardens support many local, landscape, and  
95 socio-political features that may conserve biodiversity. For instance, local features like mulch  
96 cover and flowering plant species richness augment spider activity and richness (Otoshi et al.  
97 2015). Garden size and socio-economic status of gardeners are crucial components for promoting  
98 avian richness and plant diversity (van Heezik et al. 2013). Further, urban gardens provide floral  
99 and nesting resources that may benefit insects (Wojcik et al. 2008). Individual gardens may  
100 strongly differ in management techniques and thus in vegetation and insect composition (Loram  
101 et al. 2011). For bees in particular, carefully planned, human-implemented designs can allow for  
102 local features including floral abundance, plant species richness, and appropriate plot sizes to  
103 support bee diversity and bee habitat (Frankie et al. 2005). Urban gardens are a key component  
104 to bee conservation because they can be managed for continuous floral resources (Threlfall et al.  
105 2015). But we lack information about how garden design, or in other words the spatial  
106 distribution of resources, influences bee communities (Wojcik et al. 2008).

107         In this study, we examined floral resources and bee communities in urban gardens to  
108 determine how floral abundance, floral diversity, and floral spatial distributions within urban  
109 gardens are associated with changes in bee richness and abundance. We investigated two main  
110 research questions: 1) Does bee abundance, richness, and diversity correlate with floral  
111 abundance and diversity in gardens? 2) Does the spatial distribution or connectivity of floral  
112 resources within gardens influence bee abundance, richness, and diversity? We also examined the  
113 role of floral abundance and spatial distribution in relation to other local and landscape

114 characteristics of urban gardens previously documented as important for urban bee communities.

115

## 116 **Methods**

### 117 *Study Sites*

118           We surveyed bee communities, floral resources, and other site characteristics in 18 urban  
119 gardens in Monterey, Santa Clara, and Santa Cruz Counties in the Central coast region of  
120 California during July and early August 2015 (Fig. 1). Gardens all included some vegetables, and  
121 some gardens also included a variety of ornamental, native, and non-native plants. The gardens  
122 ranged in size from 444 m<sup>2</sup> to 15,525 m<sup>2</sup>. All gardens had been in production for at least 5 and up  
123 to 47 years. At approximately the center of each garden, we established a 20 × 20 m plot in  
124 which we measured floral abundance, and in and around which we surveyed bees.

125

### 126 *Bee surveys*

127           We sampled bees with elevated pan traps and aerial nets (Grundel 2011). We constructed  
128 pan traps using 400 ml plastic bowls (yellow, white, and blue) painted with Clear Neon Brand  
129 and Clear UV spray paint and mounted each bowl to a PVC coupler with multi-purpose cement.  
130 On trapping days, we placed three 1 m tall PVC pipes in the ground in a triangle formation, 5 m  
131 apart within the 20 x 20 m plots, and placed one bowl of each color on top of 1.2 m high PVC  
132 tubes stuck in the ground (Tuell and Isaccs 2009). We placed pan traps on 8-10 July 2015  
133 between 8-9 AM and collected them (daily) between 5-7 PM. We filled bowls with a water and  
134 dish soap mixture, approximately 300 ml of water and 4 ml dish soap. At collection time, we  
135 emptied contents of each trap into containers, and then transported contents to the lab where we  
136 separated the bees from the other insects. We placed bees in vials containing 70% ethyl alcohol

137 or immediately pinned and dried bees for identification. We sampled bees using aerial nets on 7-  
138 9 July, 31 July, and 2 August 2015. We searched for and captured bees in nets for a total of 30  
139 min per site. Bees were observed on flowers, within 20 m of and inside the 20 x 20 m plots in  
140 each site. Once we observed a bee, we captured it using the aerial net, killed bees with ethyl  
141 acetate in the field, and then transported specimens to the lab for identification. We used online  
142 resources (Ascher and Pickering 2015), image databases (Packer 2015), books (Frankie et al.  
143 2014) and other dichotomous keys (Roberts 1973a; b, Michener 2007, Gibbs 2010) to identify  
144 the bees to family, genus, and species. For those bees that we were unable to identify to species,  
145 we separated genera into morphospecies. All voucher specimens are currently housed in the  
146 Philpott Lab at the University of California, Santa Cruz.

147

#### 148 *Floral surveys*

149 For floral surveys, we divided the 20 x 20 m plot into 100 2 x 2 m quadrats and assigned  
150 each quadrat a spatial coordinate (A-J, 1-10) for use in spatial analysis. Before conducting floral  
151 counts in each garden, we first spent 30-45 min observing bee foraging behavior and noting all  
152 floral species being visited by bees in that site on that day so that we only counted floral  
153 resources being used by bees in that site. Then, within each quadrat, we counted the total number  
154 of flowers, and identified all flowering plants to species or morphospecies. Flowers were  
155 individually counted and we estimated the floral abundance of inflorescences by counting the  
156 number of flowers on one inflorescence and then multiplying by the number of inflorescences in  
157 that quadrat. We also noted the color of each flower (white, yellow, purple, red, orange, dark  
158 purple, purple, or blue) in each quadrat.

159

160 ***Site characteristics***

161 As other local and landscape scale site characteristics influence bee abundance and  
162 richness within our study sites (R. Quistberg et al., *unpublished data*), we measured other site  
163 characteristics to include as explanatory variables. At the local scale, we measured ground cover  
164 characteristics. We randomly sampled four 1 x 1 m plots within the 20 x 20 m plot. Within those  
165 plots, we measured ground cover by noting the percent cover from bare soil, herbaceous plants,  
166 and mulch. At the landscape scale, we classified the land cover types surrounding each garden.  
167 We obtained land cover data from the 2011 National Land Cover Database (NLCD, 30 m  
168 resolution) (Homer et al. 2015) and calculated the percent of land cover types in 2 km buffers  
169 surrounding each study site. This spatial scale was chosen as bees have a median foraging range  
170 of 1.5-2 km (Zurbuchen et al. 2010). We used the NLCD land cover types to create four  
171 surrounding habitat categories: 1) natural habitat (including deciduous [NLCD number 41],  
172 evergreen [42], and mixed forests [43], dwarf scrub [51], shrub/scrub [52], and  
173 grassland/herbaceous [71]), 2) open (including lawn grass, park, and golf courses [21]), 3) urban  
174 (including low [22], medium [23], and high intensity developed land [24]), and 4) agriculture  
175 (including pasture/hay [81] and cultivated crop [82]). Other land cover types in the surrounding  
176 areas covered <5% of the total area and were not included. We assessed land cover with spatial  
177 statistics tools in ArcGIS v. 10.1.

178

179 ***Data Analysis***

180 The response variables in the data analyses included overall bee abundance, abundance of  
181 *Apis mellifera*, bee species richness, and bee diversity. We combined pan traps and aerial nets  
182 samples to assess total bee abundance (total number of individuals captured), *A. mellifera*



183 abundance, and species richness (total number of species captured) for each site. We calculated  
184 bee diversity with the Shannon-Wiener Index ( $H'$ ) as a diversity metric.

185 We included floral characteristics, other local factors, and landscape factors as  
186 explanatory variables in the analysis. We found a large range in all measured variables in the  
187 different study sites (Table 1). For floral characteristics, we focused on total floral abundance and  
188 richness in each study site, as well as the spatial distribution of those floral resources within  
189 individual quadrats. At the site level, we calculated the total number of flowers and flower  
190 species as well as the mean number of flowers, the max number of flowers, and the mean  
191 number of white flowers per quadrat. With the data for individual quadrats, we also calculated  
192 spatial relationships between the distributions of floral resources. With ArcGIS 10.1, we mapped  
193 the 100 quadrats for each site and joined the floral resource data to each quadrat. We focused on  
194 quadrats with  $\geq 10$ ,  $\geq 15$ ,  $\geq 50$ , or  $\geq 100$  flowers per quadrat,  $\geq 15$  white flowers per quadrat, and  $\geq 2$   
195 species of flowers per quadrat. Then, for each set of quadrats, we calculated the Nearest  
196 Neighbor Ratio (NNR) for each site to measure connectivity of these floral resources using  
197 spatial statistics from the ArcGIS 10.1. NNR calculates spatial patterns, such as clustering and  
198 dispersion. Smaller NNR values indicate a higher degree of clustering. Thus we included 5  
199 explanatory variables related to floral abundance (total floral abundance in a site, total floral  
200 species richness in a site, the mean number of flowers per quadrat, mean number of white  
201 flowers per quadrat, and the max number of flowers per quadrat), and 6 variables related to floral  
202 distribution (the NNR for quadrats with  $\geq 10$ ,  $\geq 15$ ,  $\geq 50$ ,  $\geq 100$ , and  $\geq 15$  white flowers per quadrat,  
203 and the NNR for quadrats with  $\geq 2$  species of flowers). We included 3 other local factors: percent  
204 ground cover with bare ground, percent ground cover with herbaceous vegetation, and percent  
205 ground cover with mulch. The 4 landscape explanatory variables included were percent of

206 landscape with open area, natural, agricultural or urban land use within 2 km. Thus, we included  
207 18 explanatory variables.

208         Because many of the explanatory variables may be correlated, we ran Pearson's  
209 correlations and conducted variable selection. We divided explanatory variables into four groups:  
210 1) floral abundance and richness, 2) floral spatial distribution, 3) other local factors, and 4)  
211 landscape factors, and ran Pearson's correlations for variables within each group. We examined  
212 which variables were highly correlated ( $P < 0.01$ ), and selected one of the correlated variables as a  
213 representative for subsequent analysis. For floral abundance, the mean number of flowers per  
214 quadrat was correlated with maximum flowers per quadrat (0.919,  $P < 0.01$ ), total number of  
215 flowers (0.890,  $P < 0.01$ ), and mean number of white flowers (0.875,  $P < 0.01$ ), and so we included  
216 mean number of flowers per quadrat and total flower species richness in subsequent models. For  
217 floral distribution, NNR for quadrats with  $\geq 15$  flowers was significantly correlated with NNR for  
218 quadrats with  $\geq 10$  flowers (0.936,  $P < 0.01$ ). Further, NNR for quadrats with  $\geq 50$  flowers was  
219 correlated with NNR for quadrats with  $\geq 15$  white flowers (0.905,  $P < 0.01$ ) and quadrats with  $\geq 2$   
220 species of flowers ( $-0.630$ ,  $P < 0.01$ ). Thus, we included NNR for quadrats with  $\geq 15$  flowers,  
221 NNR for quadrats with  $\geq 50$  flowers, and NNR for quadrats with  $\geq 100$  flowers in subsequent  
222 models. For other local factors, percent mulch cover was significantly correlated with percent  
223 bare cover ( $-0.784$ ,  $P < 0.01$ ), and so we included percent mulch cover and percent herbaceous  
224 cover in subsequent models. For the landscape variables, percent urban land cover was highly  
225 correlated with percent natural land cover ( $-0.911$ ,  $P < 0.01$ ), and percent open land cover ( $-0.790$ ,  
226  $P < 0.01$ ), so we included percent urban land cover and percent agriculture land cover in  
227 subsequent models. In all, 9 explanatory variables remained after variable selection.

228         We used generalized linear models (GLMs) with the glm function in R (R Development

229 Core Team 2014) to examine relationships between selected floral abundance and distribution  
230 variables, other local factors, landscape characteristics and bee abundance, richness, and  
231 diversity. We tested all combinations of different variables with the ‘glmulti’ package (Calcagno  
232 and Mazancourt 2010) and selected the top model based on the AICc values. For models where  
233 the AICc for top models was within 2 points of the next best model, we averaged models (up to  
234 the top 10 models) with the MuMIn package (Barton 2012) and report conditional averages for  
235 significant model factors.

236

## 237 **Results**

238 We collected 1,354 bee individuals from 43 species. We collected 5 bee families; the  
239 most abundant family was Apidae representing 70% of total individuals captured. The most  
240 abundant bee species was *A. mellifera* (58% of individuals captured), followed by *Halictus*  
241 *tripartitus* (10.11%), *Bombus caliginosus* (4.43%), and *Bombus vosnesenskii* (1.47%).

242 Several floral abundance, distribution, and landscape factors were included in best  
243 models, depending on the dependent variable. For the overall bee abundance, the best model  
244 only included percent urban land use within 2 km. The percent urban land use negatively  
245 correlated with the number of bee individuals ( $P=0.015$ , Fig. 2a). The best model for the  
246 abundance of *A. mellifera* included the NNR for quadrats with  $\geq 15$  flowers and percent urban  
247 land cover within 2 km. The number of *A. mellifera* individuals declined with increasing percent  
248 urban cover ( $P<0.001$ , Fig. 2b) and increased with NNR for quadrats with  $\geq 15$  flowers ( $P<0.001$ ,  
249 Fig. 2c). The best model for bee species richness included NNR for quadrats with  $\geq 15$  flowers  
250 and mean number of flowers in a quadrat in site. Bee species richness was negatively correlated  
251 with the mean number of flowers in a quadrat ( $P=0.018$ , Fig. 3a) and was lower in sites with

252 higher NNR for quadrats with  $\geq 15$  flowers ( $P=0.031$ , Fig. 3b). The best model for bee diversity  
253 included NNR for quadrats with  $\geq 15$  flowers and mean number of flowers in a quadrat. Bee  
254 diversity declined with increases in mean number of flowers ( $P=0.014$ , Fig. 3c), and declined  
255 with increases in NNR for quadrats with  $\geq 15$  flowers ( $P=0.003$ , Fig. 3d).

256 We also noted negative correlations between the abundance of *A. mellifera* and bee  
257 species richness ( $R^2=-0.561$ ,  $P<0.05$ , Fig. 4a) and bee diversity ( $R^2=-0.715$ ,  $P<0.01$ , Fig. 4b).

258

## 259 **Discussion**

260 We investigated the effect of floral abundance, distribution, and other local and landscape  
261 factors on bee communities and we found that among all variables examined, floral spatial  
262 distribution was among the important drivers of bee richness, diversity, and abundance of *A.*  
263 *mellifera*. In addition, floral abundance and urban land cover are important drivers of bee  
264 communities. Below, we discuss the results in the context of our main research questions, and  
265 also examine the results in a broader context by exploring potential interactions between *A.*  
266 *mellifera* and the rest of the bee community.

267 Bee abundance was significantly negatively correlated with the percent of urban cover in  
268 the landscape, but not with other floral abundance or distribution factors, or ground cover  
269 characteristics. Habitat loss associated with urbanization is one main cause of bee declines  
270 (Martins et al. 2013), and other studies have documented drops in bee abundance with increases  
271 in concrete, buildings, and other types of impervious cover at the landscape level (Bates et al.  
272 2011, Threlfall et al. 2015). In addition, impervious surface limits nesting opportunities for bees  
273 and can increase bee foraging distances (Fortel et al. 2014). In our study, natural and open land  
274 cover negatively correlated with urban land cover, thus impacting bee abundance positively.

275 Therefore, increases in cover by natural habitats (e.g. forest and grassland) and declines in urban  
276 developed cover promote bee abundance. For example, natural habitat provided by green roofs  
277 or small patches of ornamental plants can provide suitable habitat for bees to forage and collect  
278 floral resources (Tonietto et al. 2011, Garbuzov et al. 2015).

279 We also found that the abundance of *A. mellifera*, by far the most common bee species  
280 collected in our study, declined with increases in urban cover, increased with more dispersed  
281 floral resources, but did not respond to other local factors. Increasing amount of urban cover is  
282 implicated in declines of bee abundance, generally (e.g. Potts et al. 2010). However, *A. mellifera*  
283 usually thrives in urban green spaces such as public parks and residential neighborhoods, more  
284 so than other wild bees first because *A. mellifera* is a floral generalist and second because wild  
285 bees may lack appropriate nesting habitat in urban areas (Threlfall et al. 2015). Although many  
286 papers note *A. mellifera* as the most common bee found in urban garden studies (e.g., Tommasi et  
287 al. 2004, Matteson et al. 2008, Frankie et al. 2009), none actually examine whether landscape  
288 features correlate with *A. mellifera* abundance within urban habitats. In addition, few papers have  
289 described floral spatial distribution as an important predictor for honeybees. We found that *A.*  
290 *mellifera* abundance was higher in sites with more dispersed (i.e. less clustered) floral resources  
291 and this finding may provide insight for managing *A. mellifera* abundance in urban gardens. *A.*  
292 *mellifera* is a generalist species and its medium size permits it to forage large distances  
293 (Greenleaf et al. 2007), and thus we would expect that the species can respond positively to  
294 dispersed floral resources (Beekman and Ratnieks 2000). In another types of landscapes, *A.*  
295 *mellifera* only responded to large landscape scales and increased their density in less semi-  
296 natural habitats, thus showing adaptation to more fragmented habitats and patchy resources  
297 (Steffan-Dewenter et al. 2002). Eusocial insects, such as *A. mellifera*, that live in large colonies

298 send out numerous foragers to search for patches with abundant resources. One study reported  
299 the colony health or “energy status” of *A. mellifera* influenced the foraging distance, for instance,  
300 when the floral resources were high *A. mellifera* foraged small patches and short distances, and  
301 when resources were low they foraged longer distances and larger patches (Schneider and  
302 McNally 1992). Therefore, *A. mellifera* is more equipped to experience spatial changes in floral  
303 resources because they forage at variable distances when floral resources are also variable.

304         We also found that floral abundance and distribution of floral resources (but not  
305 landscape factors) correlated with bee species richness and diversity. We found that bee species  
306 richness and diversity was lower in sites with fewer flowers overall. Floral abundance is often  
307 implicated in increasing bee richness in urban areas (e.g. Matteson and Langellotto 2010, Wojcik  
308 and McBride 2012, Hülsmann et al. 2015). Yet, in contrast to patterns for *A. mellifera*, we found  
309 that sites with more clustered floral resources supported higher bee species richness and  
310 diversity. This is a novel finding as the first study to assess how floral distribution within urban  
311 ecosystems impacts bee communities and potentially bee conservation. Others have documented  
312 increased in abundance of individual bee groups (e.g., bumble bees) in areas with patchy floral  
313 resources (Wojcik and McBride 2012), but have not examined entire communities. Clustered  
314 floral resources may support an array of bees that forage both short and long distances, but may  
315 be particularly important for smaller bees that exhibit limited foraging ranges (Zurbuchen et al.  
316 2010). Further, different bees (even within the same genus) may respond to differently to floral  
317 patch size (Sowig 1989). The frequency of pollinator visits may decrease as flower patch size  
318 increases because searching for unvisited flowers in small patches may allow bees to optimize  
319 their foraging strategy (Goulson 2000). Similarly, floral density effects are strong at low densities  
320 because plants facilitate one another’s pollinator attraction, while higher floral densities tend to

321 have weak pollinator attraction because plants compete for pollinator attraction (Essenberg  
322 2012). Bee conservation in intensified agricultural systems (with low floral resources) can be  
323 bolstered by adding clumped spatial elements such as hedgerows or buffer strips (Klein et al.  
324 2007). These additions likely work to augment bee diversity because bees in human-managed  
325 systems respond to clustered floral resources. For example, in a different agricultural system  
326 (tropical coffee systems), bee diversity did not respond to floral resources clumping at the field  
327 scale, but bee diversity increased in sites with branch and shrub scale floral clustering, thus  
328 emphasizing the notion that responses of bee diversity to floral clustering are dependent both on  
329 floral abundance but also on spatial scale (Veddeler et al. 2006).

330         One of the striking patterns in this study is that *A. mellifera* and bee species richness and  
331 diversity responded to floral spatial distribution in opposite ways – with most bee species  
332 responding positively to clustering, and *A. mellifera* responding negatively to clustering. This  
333 prompts the question of whether interactions between *A. mellifera* and other bee species may be  
334 driving the observed patterns. We posit that due to extensive foraging ranges and generalist  
335 preferences, *A. mellifera* could be foraging in dispersed floral patches, allowing smaller bees or  
336 other bee species to occupy the clustered patches of flowers. Likewise, *A. mellifera* presence may  
337 restrict access by other bees thru interference competition, or by apparent competition if *A.*  
338 *mellifera* deplete nectar resources to the extent that other bees search elsewhere. *A. mellifera* is a  
339 suspected stressor that has influenced the interactions with other pollinators (Schweiger et al.  
340 2010). Yet there may be minimal interference of floral resources by honeybees compared to  
341 native bees because different bee groups may not share floral resources (Pedro and Camargo  
342 1991). The assumed widespread effects of *A. mellifera* on other bees are often based on  
343 observations, but not long term population assessments (Paini 2004), thus careful consideration

344 is necessary. Some studies have taken an experimental approach to examine the influences of  
345 removal of one numerically dominant bee on foraging patterns of other species. For example,  
346 removal of a numerically dominant bee (*Bombus* sp.) what is from alpine meadows in Colorado  
347 influenced the floral visitation of other pollinator species (Brosi and Briggs 2013). One  
348 experimental study demonstrated that in small and isolated flower patches, increased honeybee  
349 density reduced visitation rates, niche breadth, and reproduction of the red mason bee  
350 (Hudewenz and Klein 2015). Regardless, any interactions between *A. mellifera* and other bee  
351 species may have important implications for pollination services in urban gardens. *A. mellifera*  
352 thrives in urban settings (Tommasi et al. 2004), but their high floral visitations have led to a  
353 reduction in the fitness of native bees and the flowers other bees pollinate (Gross and Mackay  
354 1998). Generally, honeybees have poor pollination efficiency and may create discrepancies  
355 between higher bee visitation rates and lower seed sets in urban sites (Leong et al. 2014).  
356 Certainly, further research and experimentation in understanding interactions between native  
357 bees and *A. mellifera* is warranted.

358         The interaction between humans and gardens is crucial in building a strong  
359 environmental community and gardens can bring awareness to important ecosystem services  
360 achieved by sustaining biodiversity (Goddard et al. 2010). Urban gardens connect fragmented  
361 areas impacted by urbanization and intensified agriculture by linking floral communities, bee  
362 communities, and stewardship by the gardeners. The increasing issue of urbanization and loss of  
363 habitat puts significant pressures on these isolated gardens to support great diversity, thus it is  
364 crucial to study the how to diversify urban systems to promote biodiversity (Philpott et al. 2013).  
365 Our main findings show that abundance and spatial distribution of floral resources and landscape  
366 factors are important for maintaining diverse and abundant bee communities and could



367 contribute to management decisions within urban gardens. Our results suggest that bee diversity  
368 responded positively to spatial aggregations of floral resources, but that adding too many flowers  
369 all over the garden may not encourage bee species richness and diversity. Thus, gardeners might  
370 strive to plant several smaller clumped flower patches. At larger scales, promoting natural and  
371 open space within urban areas may also encourage overall bee abundance, richness, and  
372 conservation and pollination services within urban landscapes.

373

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380

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543 **Table 1.** Range of floral, ground cover, and landscape characteristics measured across 18 urban  
 544 gardens in the Central coast region of California.<sup>†</sup>

<b>Explanatory Variables</b>	<b>Min. value</b>	<b>Max value</b>
No. flowers (per 20 x 20 m plot)	789	38411
No. flower species (per 20 x 20 m plot)	5	43
No. flowers (mean per quadrat)	7.04	256.19
No. white flowers (mean per quadrat)	15.8	1065.68
No. flowers (max per quadrat)	130	7400
NNR for quadrats with $\geq 10$ flowers	1.245	1.777
NNR for quadrats with $\geq 15$ flowers	1.044	1.763
NNR for quadrats with $\geq 50$ flowers	1.02	5.737
NNR for quadrats with $\geq 100$ flowers	1.199	6.488
NNR for quadrats with $\geq 15$ white flowers	0.987	1.628
NNR for quadrats with $\geq 2$ species of flowers	1.007	3.279
Bare ground	9.62%	82.75%
Herbaceous vegetation	9.37%	85.25%
Mulch	0%	67.50%
Agricultural area within 2 km	0%	22.69%
Open area within 2 km	5.71%	29.01%
Natural area within 2 km	0%	61.20%
Urban area within 2 km	7.77%	64.76%

545 <sup>†</sup>Floral variables were measured in 2 x 2 m plots and ground cover variables in 1 x 1 m quadrats  
 546 within 20 x 20 m plots. NNR = Nearest Neighbor Ratio, smaller values show more clustered  
 547 floral resources

548 **Figure Legends**

549

550 **Figure 1.** A map of the Central coast region of California showing the 18 urban garden sites in  
551 Monterey, Santa Clara, and Santa Cruz Counties, and land cover types in the study region and  
552 surrounding the garden study sites.

553

554 **Figure 2.** Correlations showing relationships between percent urban land cover and (a) number of bee  
555 individuals and (b) number of *Apis mellifera* individuals and the Nearest Neighbor Ratio (NNR) for  
556 quadrats with  $\geq 15$  flowers and (c) number of *Apis mellifera* for bees collected in urban gardens in the  
557 Central coast region of California. The lines show the best fit and the grey area cover confidence bands  
558 based on the generalized linear models. Smaller NNR values indicate stronger floral clustering.

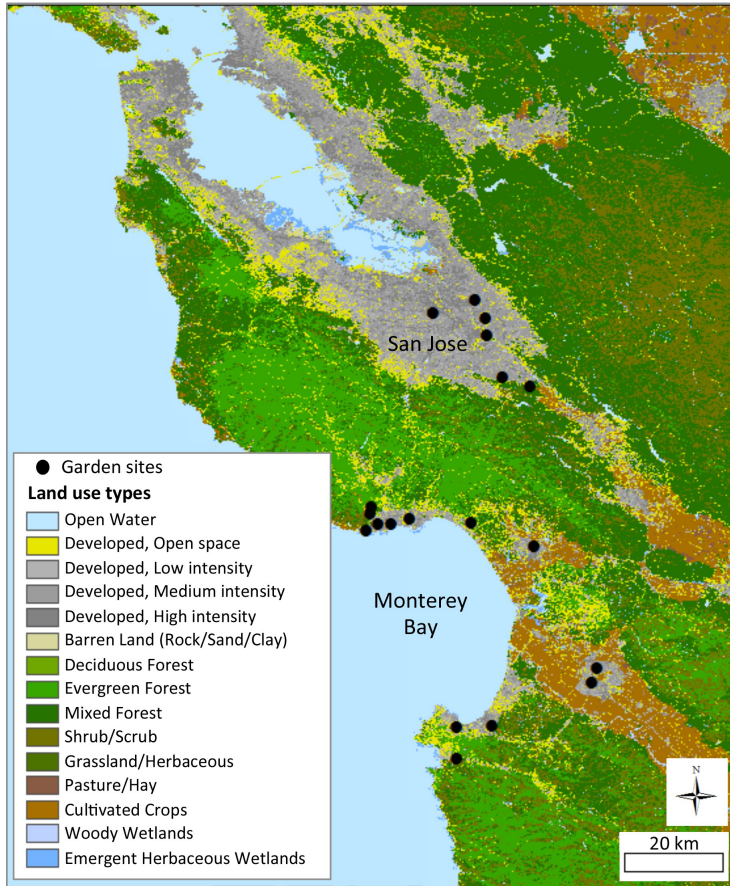
559

560 **Figures 3.** Correlations showing relationships between mean number of flowers per 2 x 2 m quadrat and  
561 (a) number of bee species and (b) bee diversity, and between the Nearest Neighbor Ratio (NNR) for  
562 quadrats with  $\geq 15$  flowers and (c) number of bee species and (d) bee diversity for bees collected in urban  
563 gardens in the Central coast region of California. The lines show the best fit and the grey area cover  
564 confidence bands based on the generalized linear models. Smaller NNR values indicate stronger floral  
565 clustering.

566

**Figure 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 cover confidence bands based on the generalized linear models.

567 **Figure 1.**

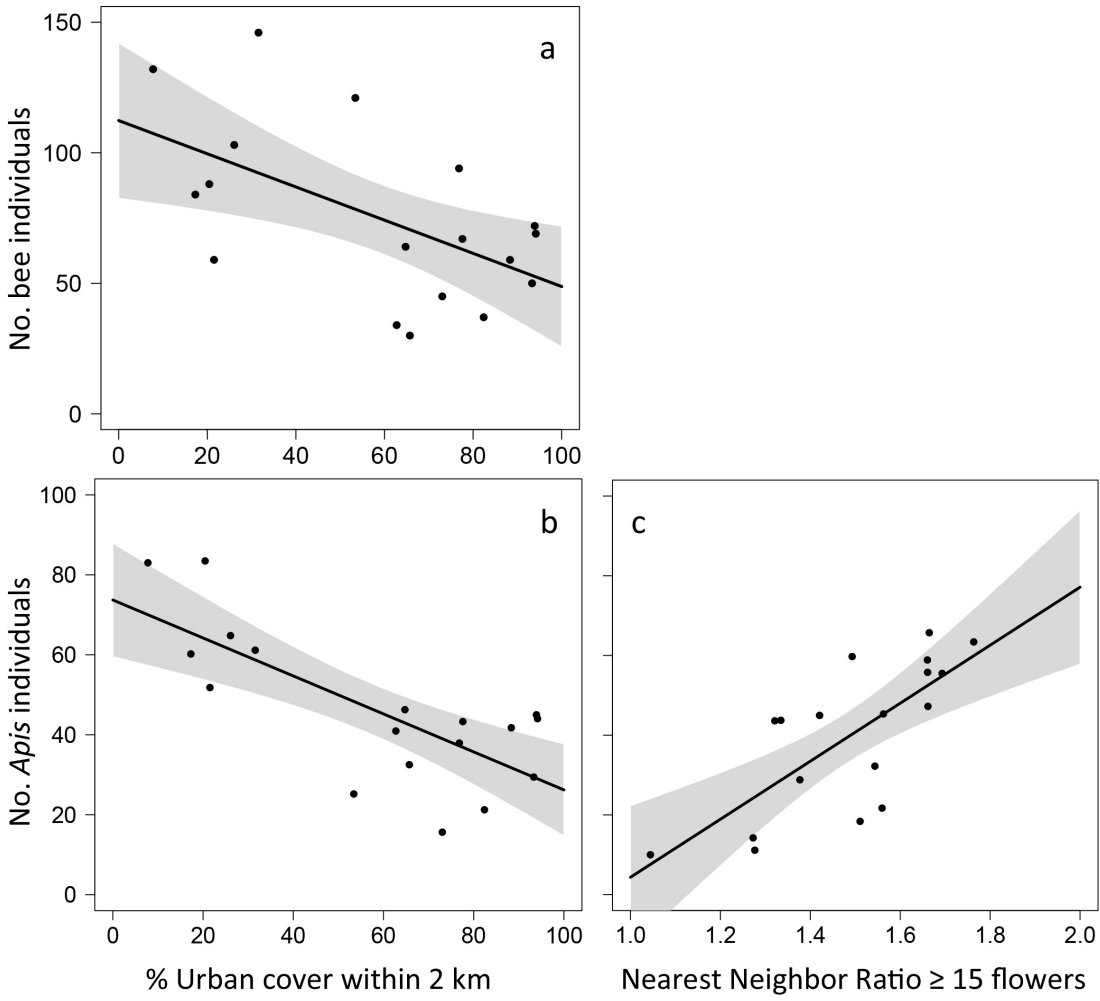


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571 **Figure 2.**

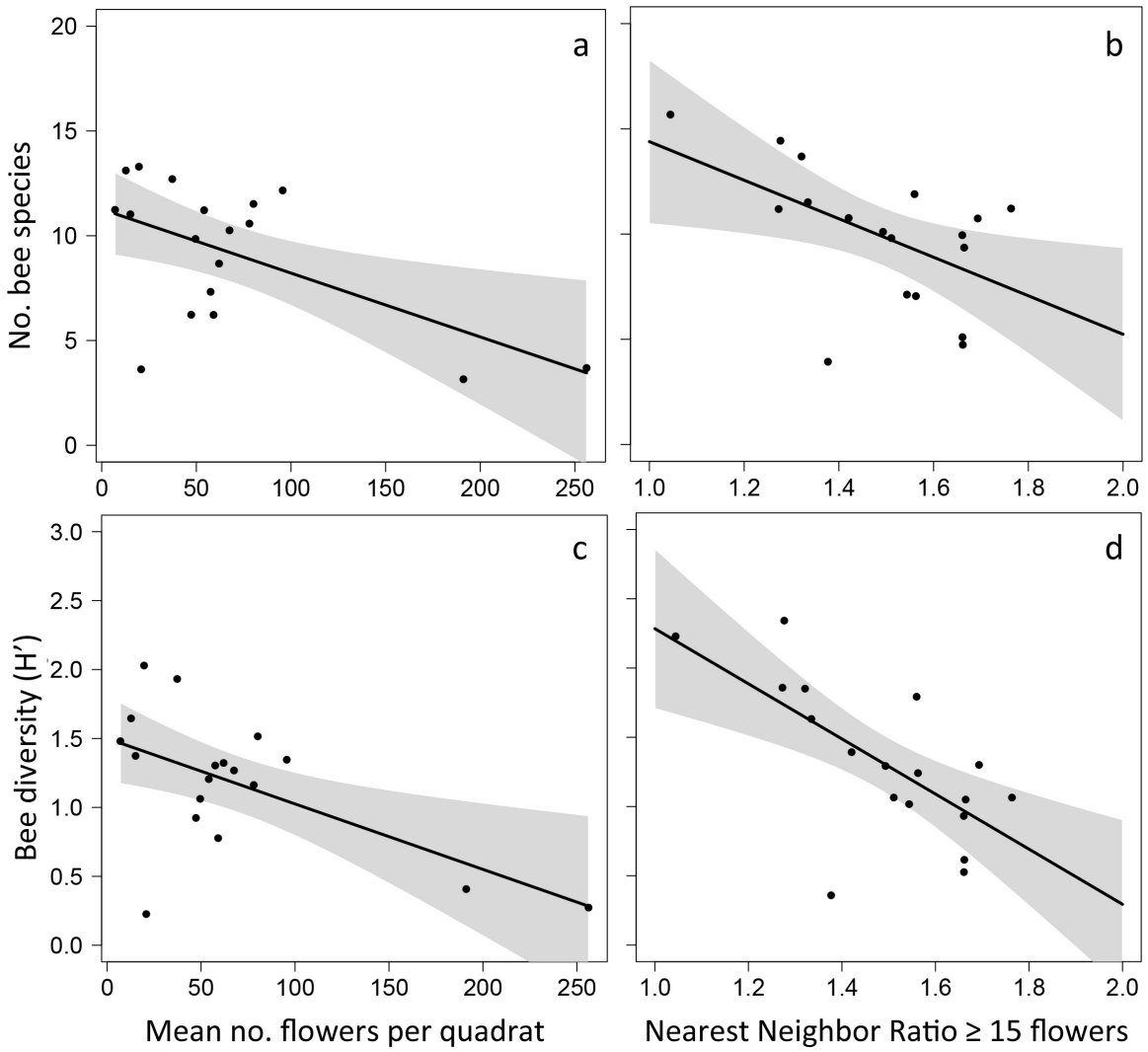


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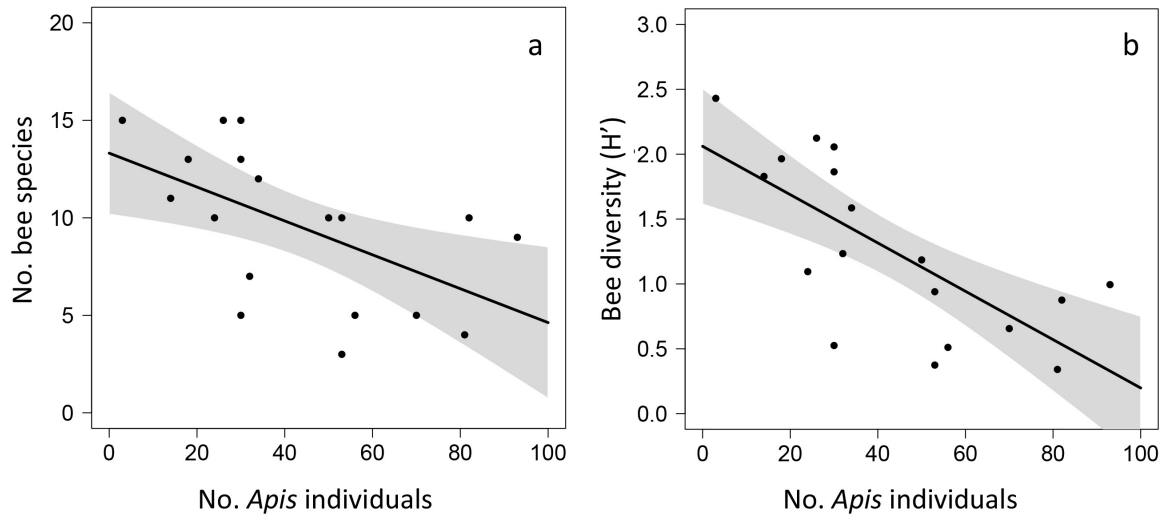
575 **Figure 3.**  
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581 **Figure 4.**

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