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## Local and Landscape Drivers of Parasitoid Abundance, Richness, and Composition in Urban Gardens

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### Abstract

Urbanization negatively affects biodiversity, yet some urban habitat features can support diversity. Parasitoid wasps, an abundant and highly diverse group of arthropods, can inhabit urban areas and do well in areas with higher host abundance, floral resources, or local or landscape complexity. Parasitoids provide biological control services in many agricultural habitats, yet few studies have examined diversity and abundance of parasitoids in urban agroecosystems to understand how to promote conservation and function. We examined the local habitat and landscape drivers of parasitoid abundance, superfamily and family richness, and parasitoid composition in urban gardens in the California central coast. Local factors included garden size, ground cover type, herbaceous plant species, and number of trees and shrubs. Landscape characteristics included land cover and landscape diversity around gardens. We found that garden size, mulch cover, and urban cover within 500 m of gardens predicted increases in parasitoid abundance within gardens. The height of herbaceous vegetation and tree and shrub richness predicted increases in superfamily and family richness whereas increases in urban cover resulted in declines in parasitoid richness. Abundance of individual superfamilies and families responded to a wide array of local and landscape factors, sometimes in opposite ways. Composition of parasitoid communities responded to changes in garden size, herbaceous plant cover, and number of flowers. Thus, both local scale management and landscape planning may impact the abundance, diversity, and community composition of parasitoids in urban gardens, and may result in differences in the effectiveness of parasitoids in biological control.

**Key words:** urban garden, parasitoid, landscape ecology, urbanization

Urbanization is a complex and dynamic process that has major effects on biodiversity and ecosystem function (McIntyre 2000, McKinney 2002). Urbanization is expected to increase worldwide as more of the human population moves into cities. As of 2014, >50% of the world's population lived in cities; a figure which is expected to grow to 66% in 2050 (United Nations 2014). The development of cities often leads to landscape modification, fragmentation, pollution, as well as the loss of biodiversity and homogenization of ecological communities (McIntyre et al. 2001, Alberti et al. 2003). In addition, urbanization creates barriers to dispersal of species across landscapes that may also negatively impact biodiversity and ecosystem services (Wiens 1976, Alberti 2005), but effects on different arthropods may depend on habitat connectivity and the overall quality of the urban matrix. As barriers to dispersal are added into a landscape, this may lower the overall quality of habitat for arthropods (Wiens 1976, McIntyre 2000). Natural enemies of pest species, including parasitoid wasps, are especially susceptible to distances between patches (Kruess and Tscharntke 1994) and decreasing patch size (Kruess and Tscharntke 2000).

Parasitoids are a highly diverse group of natural enemies in agricultural habitats, and are the most species-rich group of all Hymenoptera (LaSalle and Gauld 1993). Furthermore, parasitoid abundance and richness responds to reductions in habitat and landscape complexity. In rural agricultural areas, parasitoid abundance and richness is affected by changes to local plant and floral diversity, nectar and honeydew abundance, vegetation complexity and structure, as well as changes in landscape complexity (Marino and Landis 1996, Olson et al. 2000, Gagic et al. 2011). Likewise, in urban environments, parasitoid abundance and richness may differ with habitat type and fragment size (Gibb and Hochuli 2002), location within fragments (Christie and Hochuli 2009), as well as along an urban to rural gradient (Bennett and Gratton 2012). In some fragments within disturbed landscapes, parasitoid abundance and richness may increase in fragments due to landscape-mediated concentration (Tscharntke et al. 2012) whereby areas with relatively more resources experience short-term influx of individuals. But the temporal and spatial dynamics leading to concentration or dilution in urban areas are less understood. In addition, due to their small

size, parasitoids are unable to travel long distances to locate hosts and food resources (Olson et al. 2005), and as such parasitoids may be more affected by local as opposed to landscape characteristics (Amarasekare 2000, Bennett and Gratton 2012).

In agricultural landscapes, habitat and landscape changes, and associated shifts in parasitoid abundance, richness, and community composition may strongly alter the role of parasitoids as biological control agents of agricultural pests. Parasitoids, especially those in the Encyrtidae, Aphelinidae, and Trichogrammatidae families, are major players in control of insect pests (Goulet and Huber 1993). Ellis et al. (2005) found that by manipulating the local environment with the addition of flowering forbs there was a significant increase in the parasitism rates of bagworm larvae. Changes in the landscape may also influence parasitoids. In complex landscapes that provide refugia, parasitism rates increase (Kruess and Tscharnkte 1994, Marino and Landis 1996, Kruess and Tscharnkte 2000) sometimes, but not always leading to better biological pest control (e.g., Chaplin-Kramer et al. 2011). Yet, almost all of what is known about parasitoids and their role in biological control stems from work in rural agricultural landscapes; little is known about how changes to vegetation complexity and landscape composition may influence parasitoids and biological control in urban agricultural areas, or urban gardens. An understanding of the role of habitat and landscape complexity in driving communities of parasitoids is thus crucial to the development of effective, ecologically sound pest management strategies for those cultivating in an urban setting (Bennett and Gratton 2012, Burkman and Gardiner 2014).

Despite the abundance and diversity of parasitoids, and their importance for biological control, few have examined richness and abundance of parasitoids in urban gardens, or the management or landscape features of gardens that may drive parasitoid communities. We investigated the following: 1) How many parasitoids occur in urban gardens and which are the most common families and superfamilies? 2) Which local and landscape factors drive parasitoid abundance and richness? 3) Which local and landscape factors drive abundance of specific parasitoid superfamilies and families and changes in parasitoid community composition?

## Materials and Methods

### Study Sites

We conducted research in 18 urban gardens between 444 and 15,525 m<sup>2</sup>, and each separated by at least 2 km, located in three counties of the California central coast: Santa Cruz, Santa Clara, and Monterey (Fig. 1). Each garden is an urban community garden (managed either in allotments or collectively). Each garden contained vegetable crops and had been cultivated for between 6–48 yr. More detailed information about the original selection of the study sites, ownership regimes, and site characteristics can be found in the following publications (Otohi et al. 2015, Egerer et al. 2016, Quistberg et al. 2016).

### Vegetation Sampling

We sampled vegetation five times between June–September in 2015 within a 20- by 20-m plot placed at the center of each garden. We measured canopy cover using a concave spherical densitometer (at the center and 10 m to N, S, E, and W of center), counted and identified all trees and shrubs, and noted whether they were in flower. In four 1- by 1-m plots within each 20- by 20-m plot, we measured the height of the tallest herbaceous vegetation, identified all herbaceous plants, counted all flowers, and estimated the percent ground cover

from mulch, bare soil, herbaceous plants, and leaf litter. We also measured the size of each garden. We averaged values collected over the five sample periods. We chose to measure these variables because previous studies have documented the importance of vegetation complexity, floral abundance, and ground cover for parasitoids (e.g., Olson et al. 2000, Ellis et al. 2005, Gagic et al. 2011, Bennett and Gratton 2012).

### Landscape Analysis

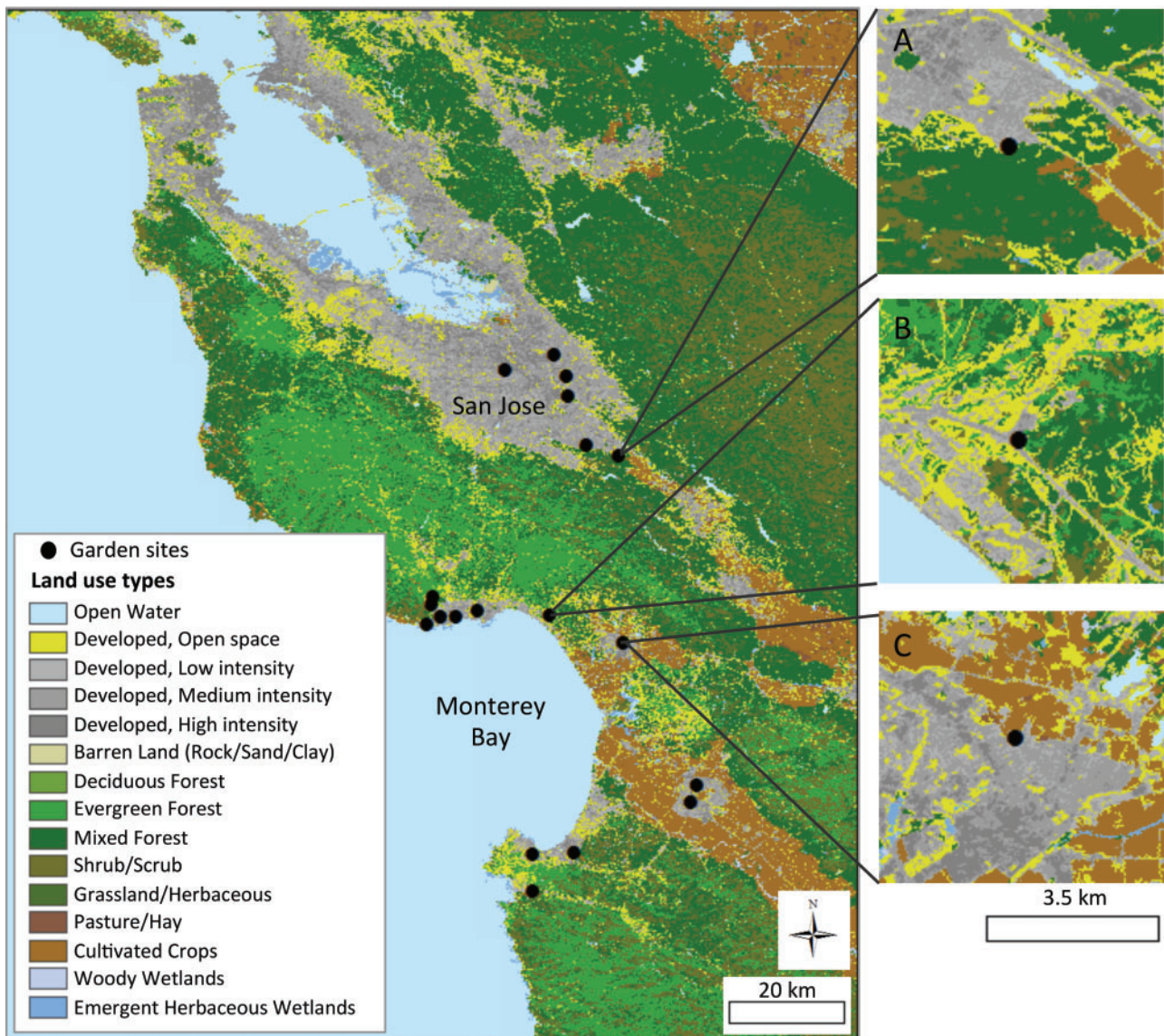
We examined the percentage of all land cover types surrounding each garden with data from the 2012 National Land Cover Database (NLCD, 30-m resolution; Homer et al. 2015). We created four habitat categories based on NLCD land cover types: 1) natural habitat (including deciduous [NLCD number 41], evergreen [42], and mixed forests [43], dwarf scrub [51], shrub–scrub [52], and grassland–herbaceous [71]), 2) open (including lawn grass, park, and golf courses [21]), 3) urban (including low- [22], medium- [23], and high-intensity developed land [24]), and 4) agriculture (including pasture–hay [81] and cultivated crop [82]). Other land cover types covered <5% of the total area and were not included. We used the “vegan” package in R (Oksanen et al. 2016) to calculate landscape diversity (a modified Shannon–Weiner diversity index ( $H'$ )). We used 500- and 1,000-m buffers to represent the scales over which small, medium, and large parasitoids can disperse for flower resources or hosts (Bennett and Gratton 2012). Thus, we included four habitat categories plus landscape diversity, each measured at two spatial scales, for a total of 10 landscape characteristics.

### Parasitoid Sampling and Identification

We collected parasitoids five times between June–September 2015 with elevated pan traps and sticky traps. Specifically, parasitoids were sampled between June 16–19, July 7–10, August 11–14, September 1–4, and September 21–24. All sample days were warm, sunny days. Pan traps consisted of 400-ml plastic bowls (yellow, white, and blue) painted with UV spray paint, filled with a solution of 300 ml water and 4 ml unscented dish soap, and placed on top of 1-m-tall PVC tubes. We chose these colors, as pan traps were simultaneously used to sample bees, although yellow is the standard for parasitoid sampling. We placed traps within 20- by 20-m plots and each trap was separated by 5 m. We placed traps between 8:00–9:00 a.m. and collected them between 5:00–6:00 p.m. We placed yellow sticky traps (15 by 20 cm) at four randomly selected locations within 20- by 20-m plots on wire stakes so that traps stayed just above vegetation. Traps were left for 24 h. All parasitoids were stored and later identified following Goulet and Huber (1993). We combined data from pan traps and sticky traps for all analysis.

### Statistical Data Analysis

We included the following dependent variables: parasitoid abundance, parasitoid superfamily richness, parasitoid family richness, abundance of common superfamilies and families (i.e., those collected from >100 individuals), and parasitoid superfamily and family composition. Because parasitoid abundance differed with study site, we only examined rarefied richness for superfamilies and families. We calculated rarefied superfamily and family richness with the individual rarefaction function and one-sigma setting in PAST (Hammer et al. 2001). For superfamilies we rarefied richness to 21 individuals and for families, we rarefied to 11 individuals to match the sites with the lowest abundances. We used natural log (LN)



**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. Three inset panels 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.

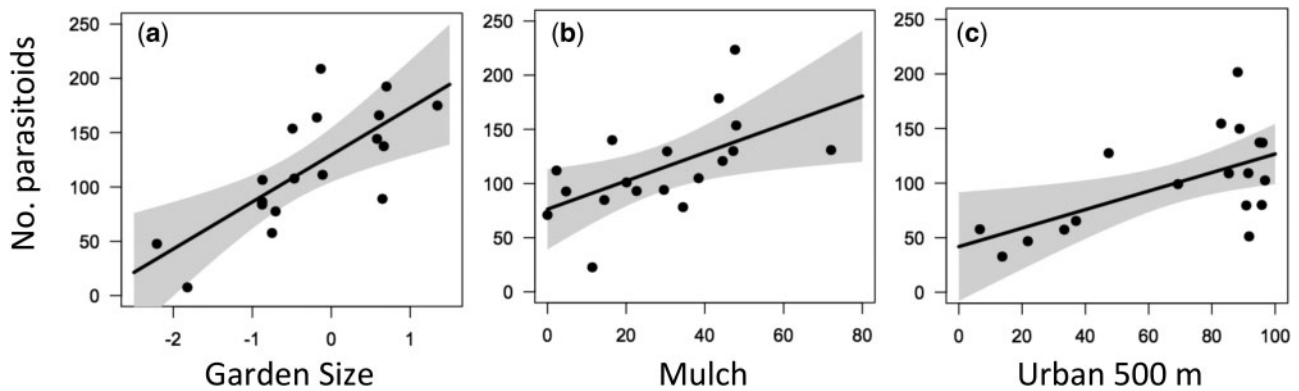
transformed values for abundance of common superfamilies and families to meet conditions of normality.

We used Pearson's correlations to limit inclusion of correlated variables in subsequent analysis. We first divided variables into three groups: 1) woody plant characters, 2) ground cover variables, and 3) landscape variables. For each group, we identified correlated variables, and of those, selected the one correlating with the greatest number of other variables or that had higher correlation coefficients (Suppl. Table 1 [online only]). For each group, we also selected all variables that were not correlated with other variables in the group (Suppl. Table 1 [online only]). Six additional variables (number of flowers, height of tallest herbaceous vegetation, herbaceous plant species richness, garden size, garden age, and county) were not placed in any group, and were also included in analysis. Thus, we included 13 explanatory variables in data analysis (Suppl. Table 1 [online only]). We used LN transformation for garden size, number of trees and shrubs, and number of flowers to meet conditions of normality.

We examined relationships between local and landscape factors and parasitoid abundance, rarefied superfamily richness, rarefied family richness, and abundance of common parasitoid superfamilies and families with generalized linear models (GLMs) in R (R Development Core Team 2014). We tested all combinations of explanatory factors using the "glmulti" package (Calcagno and Mazancourt 2012), and we compared AICc values to select the best models. 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 AICc values, *P*-values, and multiple linear model  $R^2$  values for best models. All residuals from best models conformed to conditions of normality as checked with QQ-Plots and Shapiro-Wilk tests. We graphed all significant predictors of dependent variables with the "visreg" package in R (Breheny and Burchett 2013).

To examine differences in parasitoid superfamily and family community composition, we used a permutational multivariate analysis of variance (PERMANOVA) using the "adonis" function in the





**Fig. 2.** Local and landscape drivers of parasitoid abundance in urban gardens in the California central coast as determined with GLM: (a) garden size (LN), (b) mulch cover within 1- by 1-m plots, and (c) urban developed land cover within 500 m of gardens.

“vegan” package in R (Oksanen et al. 2016). We used Bray–Curtis distances to assess dissimilarity among communities in different gardens and conducted 999 permutations. We included all 13 selected explanatory variables as potential drivers of compositional change in the PERMANOVA tests. To visualize results, we created nonmetric multidimensional scaling plots with the “ordiplot” function and superimposed significant explanatory variables with the “envfit” function in the “vegan” package.

## Results

We collected 1,820 parasitoid individuals from 8 superfamilies and 31 families and rank abundance varied with taxa (Suppl. Fig. 1 [online only]). We collected between 21 and 233 parasitoids, between 3 and 8 superfamilies, and between 4 and 19 families at each site over the summer. The most abundant superfamily was Chalcoidea (55.1% of individuals), followed by Platygastroidea (26.7%) and Cynipoidea (6.4%). The most abundant families were Scelionidae (18.7%), Mymaridae (15.6%), and Platygastriidae (8.0%).

Garden size, mulch cover, height of the herbaceous vegetation, and urban cover predicted overall abundance and richness of parasitoids. The model that best predicted overall parasitoid abundance included garden size, mulch cover, and urban cover in 500 m ( $AICc = 189.21$ ,  $df = 14$ ,  $R^2 = 0.488$ ). Parasitoid abundance increased with garden size (Fig. 2a,  $P = 0.004$ ), percent mulch (Fig. 2b,  $P = 0.033$ ), and with urban cover in the landscape (Fig. 2c,  $P = 0.026$ ). The model that predicted rarefied superfamily richness included height of the herbaceous vegetation and urban cover within 500 m ( $AICc = 28.509$ ,  $df = 15$ ,  $R^2 = 0.561$ ). Superfamily richness increased with height of herbaceous vegetation ( $P = 0.007$ , Fig. 3a) and decreased with urban cover ( $P = 0.002$ , Fig. 3b). Likewise, the model that predicted rarefied family richness included height of the herbaceous vegetation and urban cover within 500 m and also included the tree and shrub species richness ( $AICc = 27.37$ ,  $df = 14$ ,  $R^2 = 0.824$ ). Family richness increased with the height of the herbaceous vegetation ( $P < 0.001$ , Fig. 3c) and with tree and shrub richness ( $P = 0.019$ , Fig. 3e), and declined with urban cover ( $P < 0.001$ , Fig. 3d).

Abundance of common superfamilies and families varied with several local and landscape factors. Different superfamilies responded to changes in garden size, garden age, mulch cover, floral abundance, herbaceous species richness, and location (county; Table 1). Five of the six families responded to one or more local factors, three parasitoid families responded to landscape factors, two families responded to garden age, and two responded to location (county;

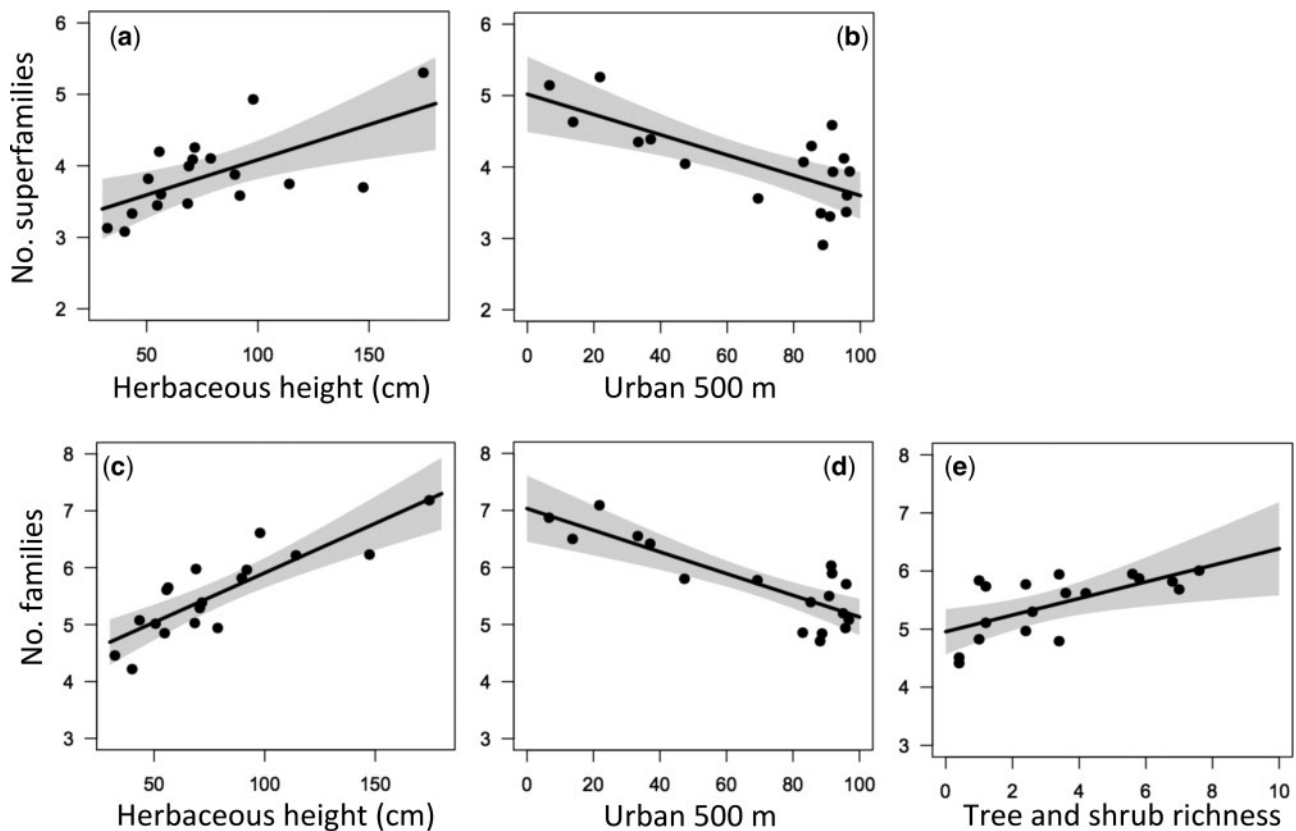
Table 1). Garden size, garden age, herbaceous species richness, urban cover, and agriculture cover all had positive effects on abundance of different superfamilies or families. Height of the herbaceous vegetation had negative effects on abundance of two families. Mulch cover and floral abundance had both negative and positive effects depending on the family.

Composition of parasitoid families and superfamilies responded to local, but not landscape effects (Fig. 4, Table 2). Family composition was significantly influenced by garden size, herbaceous plant cover, and by the number of flowers (Fig. 4a). Superfamily composition significantly varied with herbaceous plant cover, while garden size, number of flowers, and mulch cover were marginally significant predictors of superfamily composition (Fig. 4b).

## Discussion

In our study, we first describe the parasitoid communities in California central coast gardens, and then investigate which local and landscape characteristics of gardens influence abundance and family and superfamily richness, and abundance and community composition of families and superfamilies. We found that gardens harbor abundance and richness similar to other studies in urban areas, and that several local habitat features (e.g., mulch cover, herbaceous plant cover, height and species richness, floral abundance) as well as landscape features (e.g., garden size, location, urban cover) influence the abundance, richness, and community composition of parasitoids. We discuss each of these results below.

Our first research question addressed overall abundance and richness of parasitoids in urban gardens. Relatively few studies have examined patterns of parasitoid abundance or diversity in urban habitats but those that have mainly focus on examining abundance of parasitoids of a certain species or group for control of urban pests (e.g., Ellis et al. 2005), examining differences in abundance or richness along an urban to rural gradient, in different urban habitat types, or in natural habitat fragments of different sizes (e.g., Gibb and Hochuli 2002, Christie and Hochuli 2009, Bennett and Gratton 2012). Studies that do report family richness have found relatively similar numbers of families (e.g., 23 in Christie and Hochuli 2009, 29 in Bennett and Gratton 2012) and many of the same families that we identified as common in our study sites. We are not aware of comparable studies on overall parasitoid diversity in natural habitats in the study region. Nevertheless, it seems that urban gardens, collectively, may support as many superfamilies or families as other urban areas.



**Fig. 3.** Local and landscape drivers of parasitoid richness in urban gardens in the California central coast as determined with GLM. Figures show drivers of the number of parasitoid superfamilies (a, b) and families (c, d, e) as a function of herbaceous plant height in 1- by 1-m plots (a, c), urban developed land cover within 500 m of gardens (b, d) and tree and shrub richness (e).

Our second research question examined which local and landscape factors drive overall abundance and richness of parasitoids. Local factors including garden size and mulch cover predicted increases in abundance and herbaceous plant height and tree and shrub richness predicted increases in parasitoid richness. Increases in garden size may influence parasitoids either by adding resources or by contributing to more connected landscapes. An increase in the area of a garden is likely to increase the resources available to parasitoids, such as hosts and nectar-sources and may have positive impacts on landscape connectivity (Bennett and Gratton 2012). High mulch cover surrounding plants (without any increases in floral abundance over mulch) is associated with lower parasitoid abundance and parasitism in other urban habitats (Ellis et al. 2005). In our sites, mulch cover did not correlate with increases in floral abundance, yet we found positive correlations between mulch cover and parasitoid abundance. Mulch cover has both positive (e.g., spiders) and negative (e.g., bees) effects on different groups of arthropods in urban gardens (Otoishi et al. 2015, Quistberg et al. 2016), and typically mulch is applied to both retain soil moisture and suppress weed growth (Schonbeck 1999, Zehnder et al. 2007). Such changes to soils, weeds, or abundance of other arthropods may indirectly affect parasitoids. For example, increases in spider populations might reduce host abundance for parasitoids, or spiders may directly prey on parasitized arthropods. In addition, reductions in weed cover may limit abundance or diversity of alternative hosts for alternative parasitoids (Norris and Kogan 2005). Gardens both with taller herbaceous vegetation, and with higher richness of trees and shrubs (a factor correlated with increases in tree and shrub abundance as well as the abundance of trees and shrubs in flower) likely harbor much

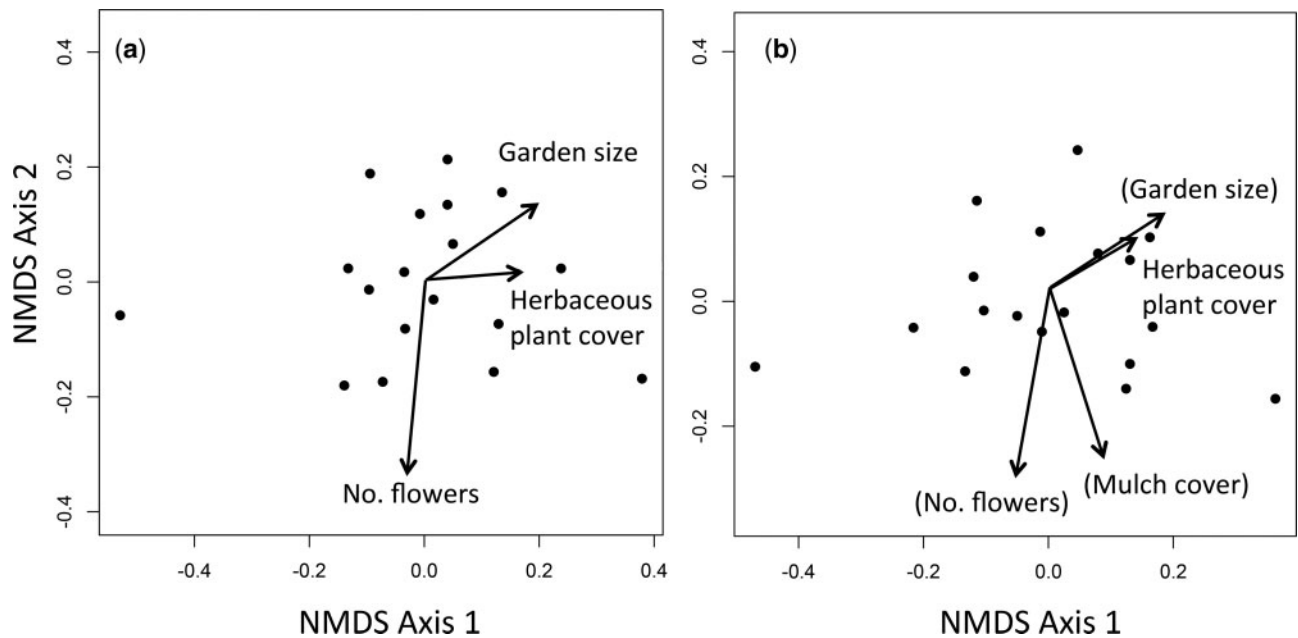
higher architectural or vegetation complexity, increases in alternative prey resources, as well as increased floral resources—factors that are all generally associated with increases in parasitoid richness (e.g., Andow 1991, Marino and Landis 1996, Landis et al. 2000, Letourneau et al. 2015), even in urban areas (Raupp et al. 2010, Bennett and Gratton 2013). However, other studies on parasitoids in urban areas have not found increases in richness with changes in local habitat features, including floral richness (Bennett and Gratton 2012).

One landscape factor, urban cover in the landscape surrounding gardens, had positive effects on abundance but negative effects both on superfamily and family richness. Increases in parasitoid abundance in urban garden sites may be due to low habitat abundance, generally, within highly urbanized landscapes. In other words, gardens may experience landscape-moderated concentration (Tschamtkke et al. 2012) because gardens are one of the few urban habitats providing a diversity of resources, compared with other, more disturbed, urban habitats. Further, abundance may be higher in those few habitat refuges due to a lack of resources in surrounding areas (Kruess and Tschamtkke 1994, Raupp et al. 2010). Other studies have failed to find differences in richness or abundance with changes in urbanization (defined as small fragments vs. large fragment interiors; Christie and Hochuli 2009). Yet, declines in parasitoid richness are consistent with other studies that have documented declines in the number of parasitoid families with increases in impervious cover (Bennett and Gratton 2012). In addition, urban cover in our landscape was negatively correlated with both natural cover and open cover in the landscape (Suppl. Table 2 [online only]), and thus changes in any of these landscape characteristics may be responsible

**Table 1.** Results of GLM predicting abundance of parasitoids in common subfamilies and families in urban gardens in the California central coast

Taxon	Predictors in best GLM model	<i>t</i>	<i>P</i>	AIC	<i>R</i> <sup>2</sup>	df
<b>Subfamilies</b>						
Chalcidoidea	Garden size	2.633	0.019	30.234	0.424	15
	Mulch cover	2.929	0.010			
Cynipoidea	Herbaceous cover	ns	ns	50.303	0.188	16
Platygastroidea	County (Monterey vs. Santa Cruz)	-3.484	0.004	9.573	0.907	13
	County (Santa Cruz vs. Santa Clara)	5.464	<0.001			
	Age	3.831	0.002			
	No. herbaceous plant species	4.385	<0.001			
<b>Families</b>						
Eulophidae	Herbaceous richness	3.004	0.009	40.506	0.561	15
	Agriculture (500 m)	2.958	0.009			
Mymaridae	Herbaceous cover	ns	ns	41.236	0.352	15
	Mulch cover	2.518	0.024			
Platygastridae	County (Monterey vs. Santa Cruz)	0.702	0.493	49.205	0.325	15
	County (Santa Cruz vs. Santa Clara)	2.596	0.202			
Pteromalidae	Garden size	3.760	0.002	41.014	0.733	13
	No. flowers	4.299	<0.001			
	Herbaceous richness	2.297	0.039			
	Urban (500 m)	2.297	0.039			
Scelionidae	County (Monterey vs. Santa Cruz)	-4.869	<0.001	-1.707	0.962	11
	County (Santa Cruz vs. Santa Clara)	7.372	<0.001			
	Age	4.962	<0.001			
	Mulch cover	-2.927	0.013			
	Height of herbaceous vegetation	-3.360	0.006			
	No. herbaceous plant species	6.113	<0.001			
Trichogrammatidae	Age	2.825	0.014	32.209	0.641	13
	Height of herbaceous vegetation	-3.042	0.009			
	No. flowers	-2.339	0.035			
	Urban (500 m)	2.322	0.037			

Factors listed are those that were included in best models, *t* and *P* values are for individual factors, and AIC, *R*<sup>2</sup>, and df are for the best models. “ns” means factor was included in the GLM best model but was not a significant driver of the dependent variable.



**Fig. 4.** Drivers of parasitoid family and superfamily community composition in urban gardens in the California central coast. Panels show drivers of (a) family composition and (b) superfamily composition as determined with PERMANOVA tests (see text for details). Variables shown in parenthesis were marginally significant correlates of superfamily composition (*P* < 0.09).

**Table 2.** Results of PERMANOVA tests examining relationships between parasitoid family and superfamily community composition and local and landscape characteristics in urban gardens

Explanatory variables	Family composition			Superfamily composition		
	F	R <sup>2</sup>	P	F	R <sup>2</sup>	P
Mulch cover (1 by 1 m)	1.57	0.06	0.147	2.78	0.09	0.060
Herbaceous plant cover (1 by 1 m)	2.29	0.09	0.029	3.43	0.12	0.033
No. of herbaceous plant species (1 by 1 m)	1.27	0.05	0.274	1.00	0.04	0.426
Height of tallest herbaceous vegetation (1 by 1 m)	1.52	0.06	0.165	1.16	0.04	0.357
No. flowers (1 by 1 m)	2.96	0.12	0.007	2.77	0.10	0.067
Canopy cover (20 by 20 m)	1.52	0.06	0.163	2.34	0.08	0.110
No. tree and shrub species (20 by 20 m)	1.02	0.04	0.436	1.10	0.04	0.380
Urban cover (500 m)	0.73	0.03	0.699	0.80	0.03	0.570
Agricultural land (500 m)	1.31	0.05	0.274	1.20	0.03	0.350
Landscape diversity (H') (500 m)	0.97	0.04	0.467	0.63	0.02	0.670
Garden size	2.53	0.10	0.020	2.57	0.09	0.090
Garden age	1.55	0.06	0.142	1.86	0.07	0.170
County	1.17	0.09	0.316	1.63	0.11	0.190

for changes in parasitoid richness. Generally, increases in urban cover or urban developed land result in declines in parasitoid richness (Bennett and Gratton 2012), whereas increases in natural habitat in the landscape, sometimes, but not always, augments parasitoid richness (Marino and Landis 1996, Landis et al. 2000, Brewer et al. 2008, Holzschuh et al. 2010, Letourneau et al. 2012). Such changes in landscapes may influence resource availability.

Finally, we examined factors that drive changes in abundance of common families and superfamilies and changes in family and superfamily community composition. Virtually every parasitoid group responded to a different set of factors, which is not surprising given that each group has a distinct natural history, different host and nectar requirements, different life histories. Abundance of several parasitoid groups and community composition responded to local habitat factors. Parasitoids were affected by changes in plant height, herbaceous plant cover, and herbaceous plant species richness. Increases in herbaceous vegetation height negatively affected two groups (Scelionidae and Trichogrammatidae). Changes in herbaceous plant cover resulted in shifts in both family and superfamily community composition. Herbaceous plant species richness was associated with increases in Eulophidae, Pteromalidae, Scelionidae, and Platygastroidea, Eulophidae principally parasitize leaf mining and wood boring Lepidoptera and Diptera, Pteromalidae primarily parasitize larvae and pupae of ants, and Scelionidae and Trichogrammatidae parasitize eggs from several insect orders (Grissell and Schauff 1990, Goulet and Huber 1993). Increases in plant height may have increased foraging time for nectar or hosts, and potentially lowering successful parasitism or population growth (e.g., Wang et al. 1997). In contrast, increases in plant cover, and especially plant richness, may have increased prey abundance or richness thus positively affecting parasitoids. In addition, higher herbaceous plant species richness could be associated with increases in nectar resources. However, the number of total flowers was a factor in surprisingly few best models considering how frequently floral nectar is cited as important for parasitoid fecundity, life span, and abundance (e.g., Ellis et al. 2005, Balzan and Wäckers 2013). Unlike Bennett and Gratton (2012) who found that parasitoid abundance increased with floral abundance, we found that the abundance of one family increases (Pteromalidae) whereas another family decreased with floral abundance (Trichogrammatidae). But changes in flower abundance did significantly influence composition of parasitoid families and had marginally significant effects on parasitoid

superfamily composition. Increases in mulch cover predicted increases in Chalcidoidea and Myrmaridae and decreases in Scelionidae, and mulch cover had marginally significant effects on superfamily composition. Mulch has both positive and negative effects on abundance and richness of other insects in the same study sites (e.g., Ootshi et al. 2015, Quistberg et al. 2016) and thus may affect host abundance for Myrmaridae and Scelionidae that parasitize insect and spider eggs (Grissell and Schauff 1990, Goulet and Huber 1993). Finally, we found that garden size influenced some parasitoids. Parasitoid composition differs in urban habitat fragments that differ in habitat type and size (Gibb and Hochuli 2002) as well as along an urban to rural gradient (Bennett and Gratton 2012). Abundance of Pteromalidae and Chalcidoidea increased with increases in garden size, and parasitoid family and superfamily composition responded to garden size. Like size influences on parasitoid abundance overall, increases in garden size may result in higher overall continuous resources, or more connected landscapes.

Abundance and composition of parasitoid families and superfamilies also shifted with differences in garden age, location, as well as the landscape surroundings of gardens. Garden age had positive effects on the abundance of Platygastroidea, Scelionidae, and Trichogrammatidae. In some studies of arthropod abundance and richness in urban areas, fragment age may have negative effects, generally, but variable effects depending on sample method or taxon (Bolger et al. 2000). They argue that populations in fragments are likely not in equilibrium, or may experience population concentration immediately following fragmentation, followed by population declines. Gardens, however, may become more vegetatively diverse and complex with time as fruit trees or ornamental plants are introduced into gardens and grow, potentially attracting higher populations of some parasitoid groups. There were significant effects of garden location (e.g., county) for Platygastroidea, Platygastriidae, and Scelionidae, with each of these groups demonstrating higher abundance in Santa Clara County compared with garden sites in Santa Cruz or Monterey Counties. Santa Clara County is a further inland site that typically experiences higher summer temperatures and less fog than the coastal sites. These temperature differences, or biogeographical effects, may have influenced the abundance of these parasitoids. Finally, changes in landscape features had different effects depending on parasitoid group. Bennett and Gratton (2012) found that abundance of several parasitoid families (e.g., Eucilidae, Encyrtidae, Braconidae, and Ichneumonidae) decline toward an



urban center, as impervious surface necessarily increases. Of the families that we also found (Scelionidae, Mymaridae, Platygasteridae), none showed changes with urban land cover. In contrast, we found increases in Pteromalidae and Trichogrammatidae abundance increased with urban cover in the landscape.

We document several local and landscape characteristics that affect parasitoid abundance, richness, and community composition, but there are still areas that deserve much more research. First, we have begun to explore the different traits (e.g., host range, nectar requirements, life history traits, ideal temperatures for population growth) that may explain the effects that we found here. However, much more detailed assessments might look systematically at the traits of different parasitoid superfamilies, families, or even species, to examine whether urban gardens act as novel ecosystems within the urban environment either attracting only species with certain traits (e.g., biotic homogenization, Smart et al. 2006) or whether gardens managed in different ways may actually increase beta-diversity within the urban jungle. In addition, although we document that parasitoids are abundant and rich within urban gardens, less is known about their potential as biological control agents in urban agroecosystems. Increased landscape complexity increases parasitism rates in agricultural systems (Marino and Landis 1996, Boccaccio and Petacchi 2009, Gagic et al. 2011) and can lead to increased complexity of host-parasitoid interactions (Tylianakis et al. 2007). Yet the relationships between natural enemy diversity and pest control are highly complex (Letourneau et al. 2009). To date, few studies have looked at any changes in parasitoid-provided biological control in urban gardens, or any changes to biological control when parasitoid abundance or richness shifts (see review in Burkman and Gardiner 2014). If gardeners are interested in promoting parasitoid abundance and richness for the sake of conservation, then they might increase the numbers of trees and shrubs in gardens and promote herbaceous vegetation, especially in highly urbanized sites where there is much impervious cover. In sum, implications for biodiversity conservation and parasitism services require further investigation.

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## References Cited

- Alberti, M. 2005. The effects of urban patterns on ecosystem function. *Int. Reg. Sci. Rev.* 28: 168–192.
- Alberti, M., J. Marzluff, E. Shulenberg, G. Gradley, C. Ryan, and C. Zumbrennen. 2003. Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. *Bioscience* 53: 1169–1179.
- Amarasekare, P. 2000. Spatial dynamics in a host-multiparasitoid community. *J. Anim. Ecol.* 69: 201–213.
- Andow, D. 1991. Vegetational diversity and arthropod population response. *Annu. Rev. Entomol.* 36: 561–586.
- Balzan, M. V., and F. L. Wäckers. 2013. Flowers to selectively enhance the fitness of a host-feeding parasitoid: adult feeding by *Tuta absoluta* and its parasitoid *Necremnus artynes*. *Biol. Control* 67: 21–31.
- Bennett, A., and C. Gratton. 2012. Local and landscape scale variables impact parasitoid assemblages across an urbanization gradient. *Landsc. Urban Plann.* 104: 26–33.
- Bennett, A., and C. Gratton. 2013. Floral diversity increases beneficial arthropod richness and decreases variability in arthropod community composition. *Ecol. Appl.* 23: 86–95.
- Boccaccio, L., and R. Petacchi. 2009. Landscape effects on the complex of *Bactrocera oleae* parasitoids and implications for conservation biological control. *BioControl* 54: 607–616.
- Bolger, D., A. Suarez, K. Crooks, S. Morrison, and T. Case. 2000. Arthropods in urban habitat fragments in Southern California: area, age and edge effects. *Ecol. Appl.* 10: 1230–1248.
- Breheeny, P., and W. Burchett. 2013. Visualization of regression models using visreg. (<http://myweb.uiowa.edu/pbreheeny/publications/visreg.pdf>), accessed 10 December 2016.
- Brewer, M., T. Noma, N. Elliott, A. Kravchenko, and A. Hild. 2008. A landscape view of cereal aphid parasitoid dynamics reveals sensitivity to farm- and region-scale vegetation structure. *Eur. J. Entomol.* 105: 503–511.
- Burkman, C., and M. Gardiner. 2014. Urban greenspace composition and landscape context influence natural enemy community composition and function. *Biol. Control* 75: 58–67.
- Calcagno, V., and C. de Mazancourt. 2012. glmulti: an R package for easy automated model selection with (generalized) linear models. *J. Stat. Softw.* 34: 1–29.
- Chaplin-Kramer, R., M. O'Rourke, E. Blitzer, and C. Kremen. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol. Lett.* 14: 922–932.
- Christie, F., and D. Hochuli. 2009. Responses of wasp communities to urbanization: effects on community resilience and species diversity. *J. Insect Conserv.* 13: 213–221.
- Egerer, M., P. Bichier, and S. Philpott. 2017. Landscape and local habitat correlates of lady beetle abundance and species richness. *Ann. Entomol. Soc. Am.* 110: 97–103.
- Ellis, J., A. Walter, J. Tooker, M. Ginzler, P. Reagel, E. Lacey, A. Bennett, E. Grossman, and L. Hanks. 2005. Conservation biological control in urban landscapes: manipulating parasitoids of bagworm (Lepidoptera: Psychidae) with flowering forbs. *Biol. Control* 34: 99–107.
- Gagic, V., T. Tschardtke, C. F. Dormann, B. Gruber, A. Wilstermann, and C. Thies. 2011. Food web structure and biocontrol in a four-trophic level system across a landscape complexity gradient. *Proc. R. Soc. B-Biol. Sci.* 278: 2946–2953.
- Gibb, H., and D. Hochuli. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. *Biol. Conserv.* 106: 91–100.
- Goulet, H., and J. Huber. 1993. Hymenoptera of the world: an identification guide to families. Centre for Land and Biological Resources Research, Ottawa, Ontario.
- Grissell, E. E., and M. E. Schauff. 1990. A handbook of the families of Nearctic Chalcidoidea (Hymenoptera). Entomological Society of Washington, Washington, DC.
- Hammer, Ø., D. Harper, and P. Ryan. 2001. PAST: paleontological statistics software package for education. 4: 9pp.
- Holzschuh, A., I. Steffan-Dewenter, and T. Tschardtke. 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps, and their parasitoids? *J. Anim. Ecol.* 79: 491–500.
- Homer, C., J. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. Herold, J. Wickham, and K. Megown. 2015. Completion of the 2011

- National Land Cover Database for the conterminous United States- Representing a decade of land cover change information. *Photogramm. Eng. Remote Sens.* 81: 345–354.
- Kruess, A., and T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological control. *Science* 264: 1581–1584.
- Kruess, A., and T. Tscharntke. 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia* 122: 129–137.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45: 175–201.
- LaSalle, J., and I. Gauld. 1993. Hymenoptera and biodiversity. C.A.B. International, Wallingford, Oxon, United Kingdom.
- Letourneau, D., S. Bothwell Allen, R. Kula, M. Sharkey, and J. Stireman, III. 2015. Habitat eradication and cropland intensification may reduce parasitoid diversity and natural pest control services in annual crop fields. *Elem. Sci. Anthropocene* 3: 000069. doi: 10.12952/journal.elementa.000069
- Letourneau, D. K., S. Bothwell Allen, and J. I. Stireman. 2012. Perennial habitat fragments, parasitoid diversity, and parasitism in ephemeral crops. *J. Appl. Ecol.* 49: 1405–1416.
- Letourneau, D. K., J. A. Jedlicka, S. G. Bothwell, and C. R. Moreno. 2009. Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 40: 573–592.
- Marino, P., and D. Landis. 1996. Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecol. Appl.* 6: 276–284.
- McIntyre, N. 2000. Ecology of urban arthropods: a review and a call to action. *Ann. Entomol. Soc. Am.* 93: 825–835.
- McIntyre, N., J. Rango, W. Fagan, and S. Faeth. 2001. Ground arthropod community structure in a heterogeneous urban environment. *Landscape Urban Plann.* 52: 257–274.
- McKinney, M. 2002. Urbanization, biodiversity and conservation. *Bioscience* 52: 883–890.
- Norris, R., and M. Kogan. 2005. Ecology of interactions between weeds and arthropods. *Annu. Rev. Entomol.* 50: 479–503.
- Oksanen, J., F. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. O'Hara, G. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2016. Vegan: community ecology package. R package version 2.3-4. (<http://CRAN.R-project.org/package=vegan>), accessed 10 December 2016.
- Olson, D., H. Fadamiro, J. Lundgren, and G. Heimpel. 2000. Effects of sugar feeding on carbohydrate and lipid metabolism in a parasitoid wasp. *Physiol. Entomol.* 25: 17–26.
- Otoshi, M., P. Bichier, and S. Philpott. 2015. Local and landscape correlates of spider activity density and species richness in urban gardens. *Environ. Entomol.* 44: 1043–1051.
- Quistberg, R., P. Bichier, and S. Philpott. 2017. Landscape and local correlates of bee abundance and species richness in urban gardens. *Environ. Entomol.* in press: doi: 10.1093/ee/nvw025.
- R Development Core Team. 2014. R: a language and environment for statistical computing, reference index version 3.1.2. R Foundation for Statistical Computing, Vienna, Austria. (<http://www.R-project.org/>), accessed 10 December 2016.
- Raupp, M., P. Shrewsbury, and D. Herms. 2010. Ecology of herbivorous arthropods in urban landscapes. *Annu. Rev. Entomol.* 55: 19–38.
- Schonbeck, M. W. 1999. Weed suppression and labor costs associated with organic, plastic, and paper mulches in small-scale vegetable production. *J. Sustain. Agric.* 13: 13–33.
- Smart, S., K. Thompson, R. Marrs, M. Le Duc, L. Maskell, and L. Firbank. 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proc. R. Soc. B.* 273: 2659–2665.
- Tscharntke, T., J. Tylianakis, T. Rand, R. Didham, L. Fahrig, P. Batáry, J. Bengtsson, Y. Clough, T. Crist, C. Dormann, et al. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.* 87: 661–685.
- Tylianakis, J., T. Tscharntke, and O. Lewis. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445: 202–205.
- Wang, B., D. Ferro, and D. Hosmer. 1997. Importance of plant size, distribution of egg masses, and weather conditions on egg parasitism of the European corn borer, *Ostrinia nubilais* by *Trichogramma ostriniae* in sweet corn. *Entomol. Exp. Appl.* 83: 337–345.
- United Nations. 2014. World urbanization prospects. Department of Economic and Social Affairs, New York, NY.
- Wiens, J. 1976. Population responses to patchy environments. *Annu. Rev. Ecol. Syst.* 7: 81–120.
- Zehnder, G., G. Gurr, S. Kühne, M. Wade, S. Wratten, and E. Wyss. 2007. Arthropod pest management in organic crops. *Annu. Rev. Entomol.* 52: 57–80.