Urban arthropods respond variably to changes in landscape context and spatial scale

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Abstract

Urbanization and urban landscape diversity influence arthropods, but the influence of landscape factors differs based on arthropod life history strategies and the spatial scale of the analysis. Most research on landscape factors has focused on one arthropod taxon or functional group, yet assessing how changes in urban landscape intensification and diversity affect several taxa across a region can inform biodiversity conservation and landscape management in times of biodiversity loss. We examined the influence of changes in urban landscape intensification and diversity across six spatial scales, from 200 m to 5 km, on the abundance and taxonomic richness of five arthropod groups in urban community gardens: ants, bees, ladybeetles, parasitoids, and spiders. We collected data over three years in 19 community gardens in the California central coast. We determined the influence of urban intensification (percent urban land-use cover) and landscape diversity (number and evenness of land-use types) on arthropod abundance and richness at each spatial scale in the context of local garden habitat. We found that all arthropod groups are influenced by landscape factors, but that landscape influence differed depending on spatial scale as well as local habitat features, likely due to arthropod community interactions and life history strategies. This study is an example of how patterns of arthropod biodiversity in urban gardens are driven by urbanization processes that shape the degree of landscape intensity and landscape diversity across spatial scales.

Key words: urbanization, arthropod biodiversity, arthropod movement, urban management

Introduction

Landscape intensification and diversity influences biodiversity and shapes ecological communities in urban landscapes. Landscape intensification in an urban context is associated with an increased percentage of impervious cover due to urbanization (Alig et al. 2004) and decreased biodiversity due to habitat loss and biotic homogenization (McKinney 2006). The degree of landscape intensification can affect biodiversity differently (Mcintyre et al. 2001), and landscape factors may or may not be strong drivers of biodiversity given a local urban habitat context. This is because uneven urbanization processes result in relatively complex landscapes that vary greatly in the amount of impervious cover, building density and urban green space composition (e.g. parks and gardens) and green space quality (Lin and Fuller 2013; Burkman and Gardiner 2014). Thus landscape diversity, measured by the number by different land-use types in an area, can be highly variable across spatial scales in urban landscapes. It is critical to determine how changes in landscape diversity and landscape intensification across space influence urban biodiversity, and to identify if and what

landscape factors are strong drivers of ecological community composition given contemporary urban biodiversity loss (Ricketts and Imhoff 2003; McKinney 2006; Flynn et al. 2009).

Biodiversity patterns across the city landscape vary along an urban to rural gradient (McDonnell and Hahs 2008; Niemelä and Kotze 2009; Burkman and Gardiner 2014) and with spatial scale (Hostetler and Holling 2000; Penone et al. 2013). For example, Penone et al. (2013) found that urbanization intensity (measured by the percentage of impervious cover) along urban railroad lines negatively affected Orthopteran abundance, richness, and traits at both large landscape scales and small spatial scales. Lizée et al. (2012) found that composition of different land-use types within a heterogeneous urban landscape influences the strength of species–area relationships for urban park butterfly communities, but that the processes affecting colonization dynamics are scale-dependent. This research emphasizes that: (1) the influence of surrounding landscape factors on urban biodiversity can vary based on the amount and diversity of urban land-use cover, as well as the study organism; and (2) there is still a need to understand how multiple landscape factors affect abundance and species diversity differently across different spatial scales in urban landscapes.

Arthropods are useful indicators of the effects of urban landscape intensification (i.e. increasing proportion of urban land-use classes) and landscape diversity (i.e. the number and relative proportions of land-use classes) on biodiversity because of their diverse life history strategies (McIntyre 2000). Arthropod foraging and dispersal strategies influence the degree to which changes in landscape affect a community and regional population (Doak et al. 1992; Kremen et al. 2007). Foraging can encompass both arthropod foraging behavior (patterns in resource access) (Grevstad and Klepetka 1992) and foraging range (the spatial scale at which arthropods move among habitats in search of resources) (Greenleaf et al. 2007). Arthropods exhibit a variety of foraging behaviors and forage at different spatial scales, from small (a couple 100 m) to large (a couple kilometers) scale ranges (Zurbuchen et al. 2010), depending on the spatial and temporal availability of resources in relation to resource requirements (Patt et al. 1997; Jha and Kremen 2013). Dispersal ability considers the ability of arthropods to move in and across space to colonize new habitat (Benton and Bowler 2012), and varies among and within arthropod groups from those that are limited in dispersal abilities (moving a couple 100 m) to those that are long-distance dispersers (moving a couple kilometers). Together, more mobile species with larger foraging ranges and long-distance dispersal abilities are likely affected by landscape changes at larger scales compared with less mobile species and vise versa (Tscharntke et al. 2005a, 2007; Benton and Bowler 2012).

In this study, we examined effects of landscape intensification and landscape diversity on the abundance and richness of different arthropod taxa in urban community gardens. Urban community gardens are parcels collectively managed by groups or allotments managed by individuals in urban areas (thereafter 'garden'). The proliferation and productivity of urban agriculture makes urban community gardens an increasingly important social and ecological component of urban green infrastructure. Urban agriculture contributes 15–20% of global food supply (Hodgson et al. 2011) and has expanded by >30% in the US alone (Alig et al. 2004). In addition, though relatively small in comparison to urban parks or forests, gardens conserve high amounts of urban arthropod biodiversity by functioning as sources of resources for foraging arthropods and as new habitat for dispersing arthropods (Goddard et al. 2010; Faeth et al. 2012).

Furthermore, arthropods play various ecosystem roles in a garden's ecological community through trophic interactions (e.g. predation) and mutualisms (e.g. pollination) that can benefit gardeners and warrant arthropod biodiversity conservation (Lin et al. 2015). We investigated the influence of landscape diversity and intensification surrounding gardens on five arthropod taxa that differ in life history strategies: ants, bees, ladybeetles, parasitoid wasps, and spiders. We asked: (1) What is the influence of urban landscape intensification and landscape diversity on the abundance and taxonomic richness of different arthropod groups in urban gardens? (2) Does the influence of these landscape factors on arthropod group abundance and richness change with changes in spatial scale? We predicted that landscape factors would differentially influence abundance and richness among arthropods and among spatial scales based on differences in arthropod life history strategies. Furthermore, we predicted that landscape factors—and particularly those at larger spatial scales—should have a greater influence on the abundance and richness of more mobile arthropods (bees, ladybeetles, parasitoids) than on less mobile arthropods (ants, spiders).

Methods

Study system

We sampled arthropods from 19 gardens in the California central coast in Monterey (36.2400° N, 121.3100° W), Santa Clara (37.3600° N, 121.9700° W), and Santa Cruz (37.0300° N, 122.0100° W) Counties (Fig. 1). We defined each garden site as a specific geographic point or coordinate in a Geographical Information Systems (GIS) database; we defined the landscape as a 200–5 km radii extent surrounding each garden. The gardens were surrounded by natural, agricultural, and urban (varying degrees of developed cover) land-uses and were intentionally chosen to reflect a gradient in landscape diversity and intensity across the central coast (Fig. 1). Gardens were >2 km apart in proximity from one another, have been in cultivation for 5–47 years, and were between 444 and 15 525 m² in size (Supplementary Table S1).

Arthropod sampling and identification

In order to assess the arthropod communities in our study system, we compiled cumulative abundance and taxonomic richness data for ants (Family: Formicidae), bees (Superfamily: Apoidea), ladybeetles (Family: Coccinellidae), parasitoid wasps (Group: Parasitica), and spiders (Class: Arachnida) in each garden. These groups are common in urban environments, have variable life history strategies, and play different roles in garden ecosystems (Table 1). We sampled arthropods during the summer over a three-year period (2013–15), during which we visited gardens five to six times per year approximately three to four weeks apart. Each taxon was sampled during one of the three years, and we collected all data on abundance and richness across all sample periods for analysis to identify cumulative patterns.

We employed multiple common sampling methods specific to each taxon. For ants, we placed six pitfall traps in two rows of three traps, with rows and traps separated by 5 m within survey plots. Traps had a diameter of 11.5 cm and depth of 7.5 cm and were buried flush to the soil surface. Traps were half filled with water and salt solution, covered with an elevated plastic plate, and left in the field for 72 h. Pitfall traps were left in the gardens
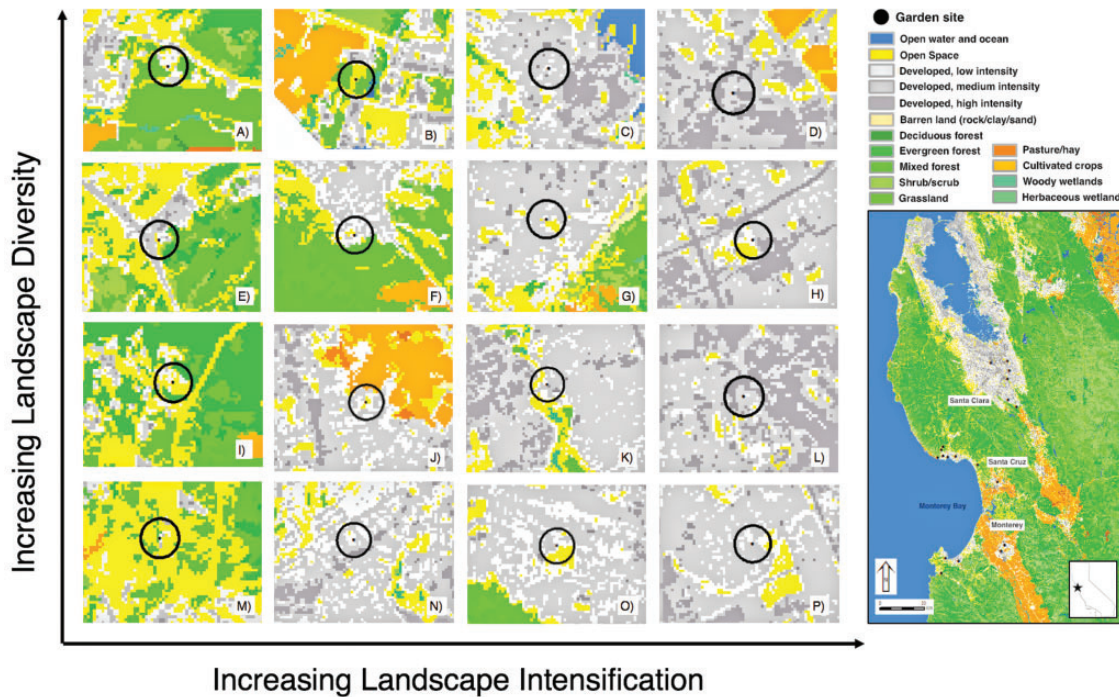
Figure 1. Garden research sites in the California central coast, USA, vary in surrounding landscape diversity and degree of landscape intensification. Dominant land-use classes consist of urban developed, natural agricultural, and open space land-uses. We present a matrix of a selected 16 garden sites (for readability) situated along a landscape diversity and intensity gradient at a 1 km spatial extent. The H' index increases along the vertical axis, and the proportion of urban land cover increases along the horizontal axis. The points indicate garden sites, and circles indicate 200 m buffer surrounding gardens (resolution 1:24 000). Full garden names and landscape factor values for each site shown is listed in Supplementary Table S1.

Table 1. Characteristics of arthropod movement (i.e. foraging distances and dispersal abilities), estimated range of movement, and the main ecosystem role(s) in agroecosystems of the five taxa examined. Species within each group play multiple roles in ecosystems; we suggest the dominant roles that groups play in gardens that are important for agricultural ecosystem services.

Taxon	Movement	Distances (m, km)	Ecological roles important for agricultural ecosystem services	Reference
Ants	Alate dispersal; central place foragers	50–100 m	Predators	Kaspari et al. 2000; Clay et al. 2010
Bees	Dispersal ability and foraging distance positively correlated with body size	Small 100–300 m; large 1.5–2.5 km	Pollinators	Kremen 2004; Greenleaf et al. 2007; Zurbuchen et al. 2010
Ladybeetles	Variable, many wide dispersers	3–5 km	Herbivore pest, mite, fungus and mildew feeders	Gardiner et al. 2009; Hagen 1962
Parasitoids	Variable, most dispersal-limited and foraging ranges a function of body size	100–500 m	Specialist predators, parasites	Roschewitz et al. 2005; Elzinga et al. 2007; Bennett and Gratton 2012
Spiders	Variable; both limited and wide dispersers, with some passive aerial dispersers	500 m to 1 km	Generalist ground-dwelling predators	Thomas et al. 2003; Sattler et al. 2010; Tscharntke et al. 2005b

during five sampling periods during 2013 (May 19–21, June 17–19, July 15–17, Aug. 11–13, Sept. 9–11). Ants were identified to species using an online guide to the ants of California (Ward 2013).

We sampled bees with both aerial netting and pan traps. We aerial netted within garden survey plots for 30 min actively searching for and capturing bees on warm, sunny days. We collected bees six times per site during 2013 (May 17–22, June 18–24, July 16–22, Aug. 12–21, Sept. 10–11, 23, Oct. 11–15). In addition, we constructed elevated color pan traps (yellow, white, and blue) painted with Clear Neon Brand and Clear UV spray paint. Traps were mounted atop 1.2 m tall PVC pipes and the pan bowls were filled with a water and soap solution (4–300 ml soap:water). On sampling days, we positioned traps (one yellow,

one white, one blue) in a triangular formation, 5 m apart within the 20 m × 20 m survey plot. Traps were left for a total of 7–11 h, set out at 8–9 AM and collected the same day between 5 and 7 PM. At collection, we emptied traps into airtight containers to transport to the lab for sorting and immediate pinning. We did these six times per garden over the summer in 2013 (May 29–31, June 25–27, July 23–25, Aug. 12–15, Sept. 17–20, Oct. 9–11). We identified bees to species using online resources (Discover Life 2013), image databases (e.g. Packer et al. 2007; Packer and Ratti 2007), books, and dichotomous keys (Michener 2007; Gibbs 2010).

For ladybeetles, we visually surveyed eight randomly selected 0.5 m × 0.5 m plots, collecting individuals on site and storing in 100 ml vials with 70% ethanol. We also placed yellow 3″ × 5″ sticky card traps on galvanized wire stakes in the ground at four random locations within the 20 × 20 m survey plot and left them for 24 h. We sampled using both methods six times in the summer of 2014 (June 17–20, July 7–10, July 27–30, Aug. 19–21, Sept. 8–10, Sept. 29–Oct. 1). Ladybeetles were identified to species using online resources (BugGuide 2003, Discover Life 2014) and Gordon (1985).

We sampled parasitoids in 2015 using pan traps (same methods as above) and yellow sticky cards (same methods as above) six times (June 16–19, July 7–10, July 31–Aug. 1, Aug. 11–14, Sept. 1–3, Sept. 21–24). We identified trapped parasitoids to family with Goulet and Huber (1993). We only identified parasitoids to family because parasitoid wasps are difficult to identify to species, especially when they are on sticky traps if the wing venation is damaged. Other studies in urban systems have also identified parasitoids to family level (see Bennett and Gratton 2012), thus making our level of sorting comparable.

Spiders were sampled using pitfall traps (same methods as above) in 2013 (same dates as above). Adult spiders in common families were identified to species, and other individuals of other families were identified to morphospecies with Ubick et al. (2005) and American Museum of Natural History Novitates (Barnes 1959; Platnick and Murphy 1984; Platnick and Shadab 1982, 1988).

Identified arthropod samples are housed in the Philpott laboratory at the University of California, Santa Cruz. We use the term taxonomic richness henceforth to refer to the respective level of identification for each taxon (ants = species, bees = species, ladybeetles = species, parasitoid wasps = family, spiders = morphospecies). We summed the number of individuals captured with any sampling method to determine total bee, ladybeetle, parasitoid, and spider abundance per year for each site for a cumulative abundance and richness value for each site for each year. For ants, we calculated abundance as ant occurrence (the presence of a species in a trap) instead of the number of individuals, which can be an inaccurate estimate of local populations (Longino et al. 2002).

Assessing landscape diversity and intensification

To answer whether differences in urban landscape intensification and landscape diversity influence arthropods, we assessed (1) the differences in landscape intensification, determined by the increasing proportion of urban developed land-use cover classes in the landscape (i.e. low, medium, high % impervious cover), and (2) the differences in landscape diversity, determined by the diversity of land-use cover classes in the landscape. To do this, we calculated the proportion (percentage) cover of each land-use class within six spatial scales surrounding gardens that we chose based on the life histories of our

study arthropods: 200 m, 500 m, 800 m, 1 km, 2 km, and 5 km. We chose a fine spatial scale of 200 m as our minimum spatial scale because it accounted for the immediate landscape area surrounding each garden that may be important for arthropods with low movement ability and short foraging distances, such as small bees (Zurbuchen et al. 2010), parasitoids (Tscharntke et al. 2005a), and spiders (Vergnes et al. 2012). Further, this scale has been defined as the edge of the surrounding landscape matrix in rural agricultural systems to assess arthropod spillover dynamics (Rand and Louda 2006). We chose a greater spatial scale of 5 km as our maximum because it accounted for the greater landscape area surrounding each garden and is a maximum foraging and dispersal range cited for many common ladybeetle species in California (Gordon 1985) and for some large bodied bee species (Zurbuchen et al. 2010). By assessing six scales we hoped to elucidate at which spatial scale effects changed and to explore why effects may differ by taxa.

We classified the surrounding landscape within buffers, or nested circles, at each of six spatial scales around each site using land cover data from the 2012 National Land Cover Database (NLCD) (Jin et al. 2013; Homer et al. 2015) and spatial statistic tools in ArcGIS version 10.1 (ESRI 2011) (Supplementary Table S2). Zonal histograms identified the total proportion cover of each NLCD land cover class present within each buffer, resulting in 12 unique land-use classes representing five broad land-use categories: (1) natural land-use classes consisting of deciduous forest [NLCD number 41], evergreen forest [42], mixed forest [43], shrub/scrub [52], grassland/herbaceous [71]; (2) urban land consisting of developed (characterized by impervious cover) low intensity [22], developed medium intensity [23], and developed high intensity [24]); (3) open land (developed open space [21]); and (4) agriculture lands consisting of pasture/hay [81] and cultivated crops [82]; (5) open water including fresh and oceanic water bodies [11] (Homer et al. 2015) (Supplementary Tables S2 and S3).

We calculated the landscape intensification surrounding each garden by summing the proportion (percentage) of urban land-use classes (developed low, medium, and high intensity) as classified by the NLCD for each spatial scale ('%Urban'). Here, a high proportion of urban land-use cover indicates higher degrees of landscape intensification, whereas a low proportion of urban land-use cover indicates low degrees of landscape intensification. We also calculated the landscape diversity surrounding gardens for each spatial scale. We used the *vegan* package in R Statistical Software (v 0.99.489) (Oksanen 2015) to calculate a modified Shannon–Wiener diversity index (H') for each spatial scale using all NLCD land-use classes. This index represents an increasing value that accounts for both richness (i.e. number of land-use classes) and evenness (i.e. weighted representation of land-use classes) of all land-use classes within each buffer. A H' value of 0 represents a simple landscape with one to few (<5) land-use classes, and a greater H' value (>2) indicates a more diverse landscape with many (>5) land-use classes with more even representation. Landscape diversity and intensification were not correlated at any spatial scale, but landscape diversity and garden size were slightly negatively correlated at 800 m and 1 km. We observed a high degree of variability in landscape factors from scale to scale for garden sites (Supplementary Fig. S1).

Habitat scale factors

To account for habitat-scale factors that may influence arthropod biodiversity, we measured the size of the entire garden, and

Table 2. The four simplified models and their derivations used in the analysis at respective spatial scales. For some arthropod groups, garden location (UTMs) is included in certain models as a coefficient (see text).

Model	Equations (200 m to 1 km)	Equations (2 km, 5 km)
Local factor only model	$Y \sim VCI + Size$	$Y \sim VCI + Size$
Landscape factor only model	$Y \sim H + \%Urban$	$Y \sim H + \%Urban + UTMs$
Landscape and local factor model	$Y \sim H + \%Urban + VCI + Size$	$Y \sim H + \%Urban + UTMs + VCI + Size$

assessed local habitat structural characteristics and vegetation complexity at each site on the same dates that we surveyed for arthropods. In four random 1 m × 1 m plots within 20 m × 20 m plots we determined abundance and richness of all herbaceous plants (including crops, weeds, ornamental plants), height of tallest herbaceous vegetation, and ground cover composition (percent bare soil, rocks, litter, grass, mulch). In addition, we measured canopy cover at five points in each 20 m × 20 m plot, and counted the number and species of trees and shrubs in the plot, and the number of trees and shrubs in flower. We averaged this habitat data at each garden across sampling periods for each site. We selected non-correlated variables important for arthropods (canopy cover, tree species diversity, crop diversity, floral abundance, percent herbaceous ground cover, height of tallest herbaceous vegetation) to create a weighted and averaged vegetation complexity index (VCI) for each garden for each year to use in the analysis (Supplemental Methods).

Model analysis

We used generalized linear regression models (GLMs) to assess the influence of urban landscape intensification and landscape diversity on arthropod abundance and taxonomic richness at the six spatial scales (Table 2). First, to be able to assess landscape and scale effects for each arthropod group we constructed a base model, one for abundance and one for richness, with only local habitat factors: garden size in acres (natural log transformed) and VCI ($n = 12$ models/group). Second, for each group we constructed four models for each spatial scale ($n = 24$ models/group): (1) arthropod abundance explained by landscape factors (%Urban, H'); (2) arthropod abundance explained by landscape and local factors; (3) arthropod taxonomic richness explained by landscape factors; (4) arthropod taxonomic richness explained by landscape and local factors. Garden buffers at 5 km scales overlapped for many sites (Supplementary Table S4), therefore, we tested for spatial autocorrelation in the residuals of linear regression models with spatial correlograms (*ncf* package) and a Moran's I spatial autocorrelation test (*spdep* package) in R (Bjornstad 2009; Bivand et al. 2012) in R (R Core Team 2016). We added garden location (Universal Transverse Mercator (UTM) coordinates) for all models at 2 km and 5 km scales, as well as for models <2 km where we found spatial correlation (Supplementary Table S5). We included these larger spatial scales in the analysis, while accounting for spatial autocorrelation by including UTM coordinates, due to the potential importance of that spatial scale for arthropods.

For ants, we included Argentine ant (*Linepithema humile*) abundance as a covariate in all models with local factors due to the high abundance within our samples that may dilute detectable landscape factor signals. Thus the response variables in the models included the following arthropod variables: ant occurrence and taxonomic richness, bee abundance and taxonomic richness, ladybeetle abundance and taxonomic richness,

parasitoid abundance and taxonomic richness, and spider abundance and taxonomic richness. Arthropod abundances were natural log-transformed to meet assumptions of normality. We used model AIC values to assess the influence of landscape factors, considering the best fit models to have the lowest AIC scores. We identified the best fit model across all and within each spatial scale for each arthropod group. All model analyses were performed using R Statistical Software (v 0.99.489) (R Core Team 2016).

Results

Overall, we collected eight species of ants and 343 occurrences; 55 species and 2062 individual bees; 14 species and 635 individual ladybeetles; 33 families and 1801 individual parasitoids; and 22 families, 46 morphospecies, and 1549 adult individual spiders. The most common ants are *L. humile* (Argentine ant; 50.8% of all occurrences), *Cardiocondyla mauritanica* (16.9%), *Hypoponera opacior* (14.6%), *Tetramorium caespitum* (10.3%), and *Nylanderia vividula* (4.95%). The most common bees are *Halictus tripartitus* (39.3% of all individuals), *Apis mellifera* (32.9%), *Lasioglossum* spp. (8.1%), and *Bombus vosnesenksii* (3.7%). The most common ladybeetles are *Psyllobora vigintimaculata* (67.4% of all individuals), *Stethorus* spp. (9.2%), *Harmonia axyridis* (6.7%), and *Hippodamia convergens* (3.6%). The most common parasitoids are Chalcidoidea (55.6% of individuals), Platygastroidea (27.0%), Cynipoidea (6.6%), and Ichneumonoidea (4.8%). The most common families of spiders are Lycosidae (64% of individuals) and Gnaphosidae (17%), commonly known as wolf and ground spiders, respectively (Supplementary Table S6).

Our first question addressed the influence of urban landscape intensification and landscape diversity for different arthropod groups. We found that changes in landscape intensification and diversity had varying influence on arthropods, but that landscape factors were important for all groups at either most or all spatial scales (Figs 2 and 3; Supplementary Tables S7–S9).

Ant abundance was best predicted by the local factor only model (including VCI, garden size, Argentine ant abundance) at all spatial scales (Fig. 2a), where Argentine ant abundance drove decreases in ant abundance. Ant richness was similarly predicted by the local factor only model but landscape factors (H', %Urban) became important from 500 m to 1 km (Fig. 3a), where increased %Urban, H' and Argentine ant abundance drove decreases in ant richness.

Bee abundance was best predicted by landscape (H', %Urban) and local (VCI, garden size) factors at 800 m (Fig. 2b). Overall, the addition of landscape factors with local factors better explained bee abundance through 1 km, but landscape variables did not further explain variation in bee abundance at larger spatial scales. Both increased %Urban and H' drove decreases in bee abundance from 500 m to 1 km, while increased garden size drove increases in bee abundance at 500 m (Supplementary
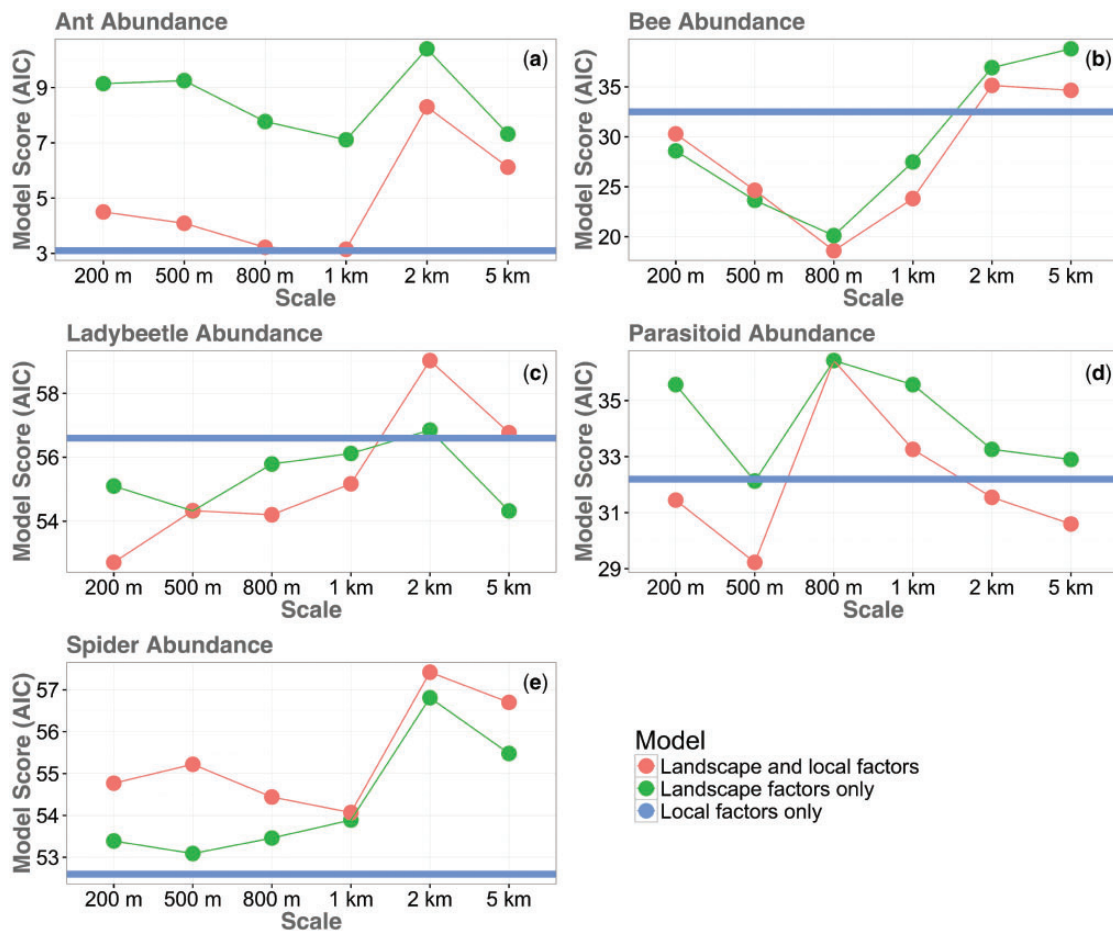
Figure 2. Visualization of model score (AIC) as a function of spatial scale for ant (a), bee (b), ladybeetle (c), parasitoid (d), and spider (e) abundance. Solid line indicates local factor only model. Scores change in response to changes in spatial scale. Visualizations and coefficient values of best fit models available in Supplementary Information.

Fig. S2). The best model that predicted bee richness included landscape factors (H', %Urban, UTMs) at 5 km (Fig. 3b) (Supplementary Fig. S3).

Ladybeetle abundance was best predicted by local and land-scape factors, but it varied based on spatial scale (Fig. 2c): local factors influence abundance until the largest spatial scale, at which only landscape factors (H', %Urban, UTMs) predicted variation in increased ladybeetle abundance. The best model for ladybeetle richness was the local model (VCI, garden size), where richness increased with increased VCI and garden size.

Parasitoid abundance was best predicted by landscape factors at small spatial scales (200–500 m) and then again at larger scales (2–5 km) (Fig. 2d). Parasitoid richness was not influenced by landscape factors, and was best explained by the local factors (VCI, garden size) across spatial scales (Fig. 3d), where increased garden size drove increases in parasitoid richness (Supplementary Fig. S3).

Spider abundance was best explained by local factors (VCI, garden size) at all spatial scales (Fig. 2e). Yet landscape factors best predicted spider richness across all spatial scales (Fig. 3e), where H' and %Urban drove decreases in spider richness at most spatial scales (Supplementary Fig. S3).

Please see Supplementary data (Supplementary Tables S7–S9; Figs 2 and 3) for model AIC values, information on model coefficients, model visualizations and the directionality of relationships.

Discussion

The landscape surrounding gardens was an important predictor of the abundance and richness of arthropod communities within gardens, yet its influence varied as a function of spatial scale, local variables and arthropod group. We found that more mobile arthropods are more affected by changes in landscape intensification and diversity at mid to large spatial scales, while less mobile arthropods are influenced more so by local habitat factors across scales. In addition, local garden factors may become more important for mobile groups at spatial scales related to dispersal and colonization strategies of arthropods if urban landscape factors hinder movement.

For more mobile arthropods like bees and parasitoids, increasing landscape intensification negatively affected groups at scales corresponding to dispersal and central place foraging ranges (≤ 2 km) (Kremen et al. 2004; Zerbuchen et al. 2010; Bennet and Gratton 2014). This suggests that more intensive urban landscapes are impeding mobile arthropod movement and leading to population decline. Bees declined with landscape intensification across small to mid spatial scales, likely because
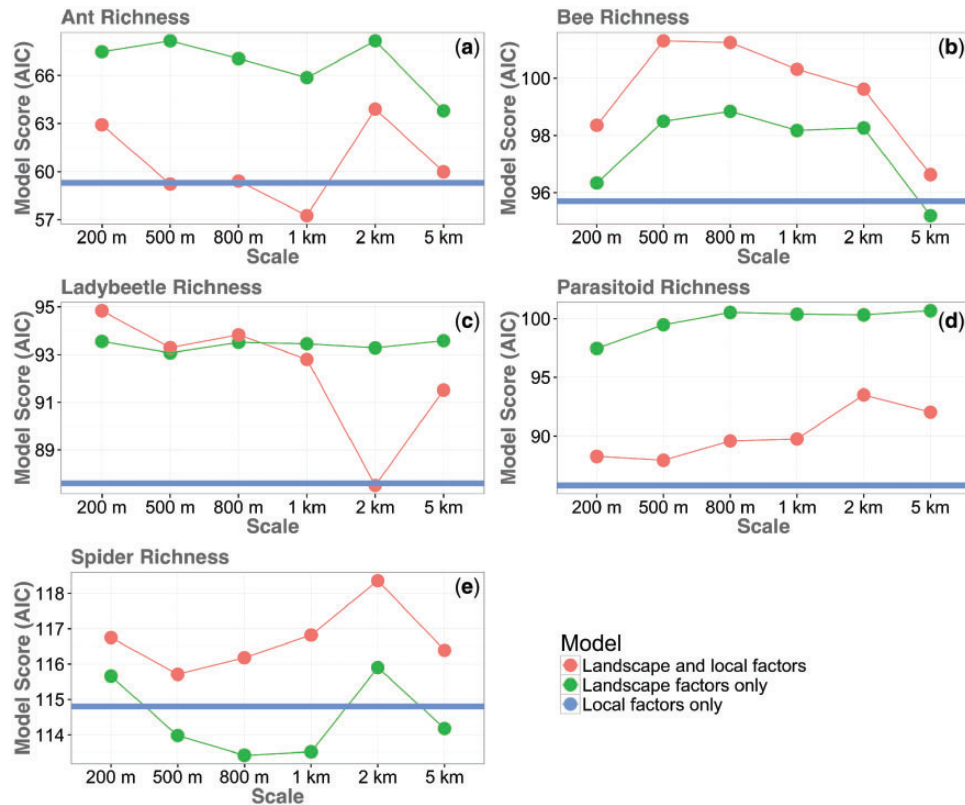
Figure 3. Visualization of model score (AIC) as a function of spatial scale for ant (a), bee (b), ladybeetle (c), parasitoid (d), and spider (e) taxonomic richness. Solid line indicates local factor only model. Scores change in response to changes in spatial scale. Visualizations and coefficient values of best fit models available in Supplementary Information.

the most abundant bees in gardens (*Halcitis*, *Apis*, and *Lasioglossum* species) have relatively small foraging ranges (<1 km) (Zerbuchen et al. 2010). Landscape driven parasitoid population decline was most prominent at small spatial scales and again at large spatial scales likely because small to large-sized parasitoids were affected by landscape intensification (Bennett and Gratton 2012), and because of an interaction with landscape diversity and local habitat factors (garden size) at mid range scales. While landscape intensification effects were similar, landscape diversity had differential effects on mobile arthropods: while bees declined with increasing diversity, parasitoids increased in diverse landscapes (e.g. Fig. 1D, K). This suggests that landscape-moderated concentration (Tscharntke et al. 2012)—due to higher landscape diversity and increased garden size—countered negative influences of urban landscape intensification to sustain parasitoid populations. We found similar concentration effects for ladybeetle abundance and richness, both of which increased with increased landscape diversity and also intensification, suggesting gardens with diverse landscape surroundings provision resources and habitat but that some ladybeetles may be more adapted to urbanization (Roy et al. 2016).

For less mobile species like spiders, landscape intensification may decrease dispersal to gardens from source habitats to decrease species richness. Increased urban cover decreased spider richness, likely because spiders rely on agricultural and natural habitat (inversely related to agricultural land-use) for maintaining populations. Lycosidae (wolf spiders)—the most abundant spiders in our gardens (Otoshi et al. 2015)—are often

the first to colonize agroecosystems (Royauté and Buddle 2012) and their dispersal from source agricultural habitats to surrounding habitats is important for maintaining populations (Bang and Faeth 2011). While ground-foraging spiders (Otoshi et al. 2015) and web-building spiders (Langellotto and Denno 2004; Shrewsbury and Raupp 2006) may respond differently to landscape factors, spider richness in this system is likely mediated by the urban landscape facilitating or hindering dispersal.

Yet, landscape effects may be indirect for less mobile arthropods. The presence of the Argentine ant along with increasing urban landscape intensification and diversity negatively affected ant communities. The Argentine ant proliferates in urban landscapes by exploiting small urban habitat patches, displacing native ant species that have larger habitat requirements, and interfering with native ant foraging behavior to decrease ant community richness (Human and Gordon 1997). Urbanization limits native ant foraging and dispersal (Buczkowski and Richmond 2012), thereby decreasing their ability to disperse from Argentine ant competition. Our findings demonstrate the relationships among increasing landscape intensification, greater Argentine ant abundance, and decreased native ant abundance and richness.

The caveats of our study are that (1) we did not detect spatial relationships between arthropod groups and landscape variables due to the inability of land cover data to capture the nuances of the urban landscape, and (2) our landscape intensification measurement included all urban land covers, regardless of intensity. Urban landscapes are relatively complex in their land-use composition, setting them apart from

agricultural landscapes. Spaces such as city parks, botanical gardens, home gardens, and flowers and trees along city streets and in yards can provide resources for arthropods that lessen the effect of landscape intensification by increasing urban landscape matrix quality (Smith et al. 2006; Hernandez et al. 2009). Land cover resolution used here and in most landscape scale analyses from urban areas (30 m) is not really differentiating these highly heterogeneous urban environments. In our study landscapes, our anecdotal observations were that even categorized 'highly developed' urban areas with high density housing can have high amounts of floral, tree, and shrub diversity. California's central coast climate allows for nearly year-round favorable growing conditions, and many residents grow a variety of plants and crops within their small yard spaces. The quality of the surrounding landscape is important for arthropods (Smith et al. 2006; Bennett and Gratton 2012; Jha and Kremen 2013; Lin and Fuller 2013), where increasing quality (through increased resource and habitat availability) decreases barriers to movement (Vandermeer and Carvajal 2001). Biodiversity within gardens can be influenced by the quality of the green infrastructure within the urban landscape surrounding gardens that satellite imagery does not detect. Thus, including all urban land-use classes, regardless of intensity, into one landscape measurement may potentially further dilute landscape intensity and mask landscape quality at scales important for arthropods.

Conclusion

Urban community gardens harbor diverse arthropod communities. Research that assesses the impacts of a range of spatial scales and landscape contexts on multiple taxa in gardens strengthens our understanding of arthropod biodiversity across city landscapes and can inform urban conservation and management practices (Fuentes-Montemayor et al. 2012). In gardens, all five of these arthropod groups play important ecological roles and provide gardeners a suite of ecosystem services like pollination or pest and disease control that contribute to food production. Given the sensitivity in urban landscape intensification that some arthropods face, we conclude with several suggestions. From a research perspective, the next steps in urban garden research should experimentally measure the influence of landscape factors on ecosystem service provisioning by arthropods to link arthropod biodiversity conservation to ecosystem services. In addition, future research should explore how arthropods are moving to and from gardens as we know little about how movement patterns may be altered in urban landscapes. This can inform the mechanisms behind correlative relationships among arthropods and landscape factors. From a management perspective, regional urban planners should consider the life history strategies of multiple beneficial arthropods when deciding on garden site location if they aim to conserve urban biodiversity. Further, gardeners should consider how garden arthropod biodiversity is influenced by the landscape surrounding their gardens when deciding how to cultivate and manage their plots. For example, if able, gardeners in smaller gardens in more intensive urban landscapes should try to increase vegetation complexity at the plot scale and garden habitat scale to provision for many arthropod groups. Yet gardeners practicing in larger gardens can also recognize the potential importance of their gardens as large habitat islands and reservoirs of biodiversity that spillover to the surrounding landscape. Together, connecting landscape research on arthropods to garden management can facilitate conservation efforts of biodiversity in urban gardens that benefit human and non-human communities in cities.

Data availability

All data used in this study is available upon reasonable request. All arthropod specimens are housed in the Philpott Laboratory at University of California, Santa Cruz where they are available for study.

Supplementary data

Supplementary data are available at *JUECOL* online.

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