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Cityscape quality and resource manipulation affect natural enemy biodiversity in and fidelity to urban agroecosystems

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Abstract

Context Complex landscapes with high resource availability can support more diverse natural enemy communities and better natural pest control by providing resources and facilitating organism dispersal. Moreover, in agricultural landscapes, local agroecosystem management can support biodiversity maintenance and pest control by adding resources in less complex landscapes with fewer resources. However, we lack an understanding of how local and landscape factors interact to affect natural enemy communities and their site fidelity to agroecosystems in urban landscapes (i.e., cityscapes).

Objective To better understand how local and landscape factors influence natural enemies in urban agroecosystems, we used urban community gardens as a model system to test if and how local resource manipulation and differences in cityscape quality affect natural enemy (ladybird beetles, parasitoid

wasps) communities and their fidelity to urban habitats.

Methods We performed two manipulations. First, we added local floral resources in 6 of 12 gardens situated in different cityscapes to measure differences in natural enemy biodiversity. Second, in those 12 gardens, with and without resource additions, we manipulated populations of a common natural enemy, *Hippodamia convergens*, to assess fidelity to the gardens.

Results Floral resource additions increased parasitoid abundance and changed community composition, but had little effect on ladybeetle abundance, richness or site fidelity. Rather, ladybeetle fidelity to gardens was lower in gardens in low quality cityscapes with high impervious cover.

Conclusions Cityscape quality influences natural enemies in and fidelity to gardens. Landscape-moderated biodiversity patterns observed in rural landscapes likely differ from urban contexts with implications for pest control.

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Introduction

Landscape compositional heterogeneity affects population dynamics, biodiversity conservation, and ecosystem services in agroecosystems by influencing the availability and spatial distribution of resources (Denys and Tscharntke 2002; Rourke et al. 2011). Diverse landscapes with more mixed land cover types are high quality landscapes that generally support a greater diversity of species by providing different resources for different organisms (Tscharntke and Brandl 2004), especially for mobile organisms with complex life histories (e.g., pollinators, natural enemies) (Kremen 2005; Chaplin-Kramer et al. 2011). More simple landscapes with fewer resources, in contrast, are low quality landscapes and may contain high barriers to dispersal and may increase the fidelity of individuals to habitat fragments (Fahrig 2003). Resource availability in the landscape therefore determines landscape quality and drives dispersal and colonization patterns (Schellhorn et al. 2015a), but interactions between landscape quality and local habitat management can influence populations, their dispersal, and service provisioning (Martin et al. 2016). Local habitat manipulation (e.g., through plant resource additions) can increase habitat quality, better support biodiversity and thereby can enhance ecosystem services in simple, low quality landscapes (i.e., the intermediate landscape complexity hypothesis) (Tscharntke et al. 2012). However, the positive effect of local resource manipulation on biodiversity and service provisioning can be relatively less impactful in already high quality landscapes composed of mixed land cover types. This is because high quality landscapes support dispersal between patches and maintain high regional (beta) diversity everywhere; in addition, high quality landscapes can provide spatial insurance in ecosystem function through high beta diversity maintenance if there is a local environmental disturbance or change in local management (i.e., the landscape-moderated insurance hypothesis) (Loreau et al. 2003; Tscharntke et al. 2012; Gámez-Virués et al. 2015). Thus, as for systems in other landscapes, landscape-scale processes can have strong effects on biodiversity, function, and services in agroecosystems.

While local and landscape drivers of agroecosystem biodiversity and dispersal in rural landscapes are increasingly understood (Rourke et al. 2011; Martin

et al. 2016), we still need to better understand how local and landscape factors interact in urban landscapes – what we term ‘cityscapes’. Cityscapes are increasing in global cover, and are novel in their landscape-scale heterogeneity (in land cover) and in local-scale habitat management (Cadenasso et al. 2007; Kowarik 2011). Local and landscape factors inconsistently affect biodiversity in cityscapes, likely due to landscape-scale habitat loss, fragmentation, and frequent disturbance that in turn affect organism dispersal and use of urban habitats (Angold et al. 2006). For example, in urban gardens, increasing garden vegetation complexity through floral resource addition may (Pawelek et al. 2009) or may not (Matteson and Langelotto 2009) enhance beneficial insect diversity in cityscapes with high amounts of impervious cover (i.e., concrete and built impermeable surfaces) that may be of low quality. The effects of cityscape quality and local management on biodiversity are likely explained in large part by their effects on organism dispersal. For example, high impervious cover may hinder dispersal and may increase site fidelity of individuals to a habitat if emigration is associated with increased mortality risk in a low quality hostile matrix (i.e., low quality land cover in which habitat patches are embedded) (Fahrig 2001). In contrast, cityscapes of higher matrix quality with more natural vegetation cover may facilitate dispersal, resulting in lower site fidelity of individuals to habitats but overall high landscape connectivity through their movement. However, there is little to no information on arthropod population movement in cityscapes or regarding how cityscape quality may trigger or hinder dispersal from urban ecosystems.

In this study, we use urban agroecosystems (community gardens) to test if and how local habitat manipulation and differences in cityscape quality affect natural enemy communities and their fidelity to urban habitats. In our study system, there are strong but variable landscape-scale effects on natural enemy biodiversity (Egerer et al. 2017). Indeed, gardens in low quality cityscapes (i.e., with greater amounts of impervious land cover) generally have higher abundance and species richness of ladybeetles (Egerer et al. 2016), counterintuitive to aspects of island biogeography theory that would predict lower abundance and richness in smaller fragments farther away from other greenspaces (MacArthur and Wilson 1976). Yet for gardens in high quality cityscapes (i.e., with greater

natural land cover), local factors like greater floral abundance and greater grass groundcover increase natural enemy abundance and species richness, respectively, likely by providing necessary food and shelter across life stages (Egerer et al. 2016). An interplay among local and landscape factors is affecting natural enemy dispersal behavior and the fidelity to gardens, but we still do not know the mechanisms driving these patterns. This information is significant because factors that affect natural enemy dispersal and site fidelity can affect pest control services (With et al. 2002), and therefore have important implications for improving sustainable pest control through habitat management in urban agroecosystems.

We conducted two manipulation experiments to test if and how differences in cityscape quality and local resource availability influence the abundance, diversity, composition, and site fidelity of natural enemies (ladybeetles, parasitoid wasps) in and to gardens. First, we manipulated garden floral resource availability to ask whether local resource (floral) additions affect the abundance, diversity, and composition of ladybeetle and parasitoid communities. Here, we hypothesized that the addition of floral resources will have a stronger influence on the abundance, richness, and composition of natural enemy communities in low quality cityscapes because added floral resources provide important food (nectar, pollen) and habitat within the garden that is less abundant in the surrounding impervious matrix. Second, we did a mark-recapture experiment of a common ladybeetle species to ask whether local resource manipulation and cityscape quality affect the site fidelity of ladybeetles to gardens. Here, we hypothesized that (i) local resource manipulation will have a stronger influence on ladybeetle fidelity to gardens in low versus high quality cityscapes through local resource provision that slows dispersal; and (ii) high quality cityscapes will facilitate dispersal due to abundant resources in the landscape, and gardens in high versus low quality cityscapes will have lower site fidelity of beetles. Together, the two experiments organized around predictions of landscape moderated biodiversity (*sensu* Tscharntke et al. 2012) aimed to determine if the effect of local manipulation on natural enemy communities or fidelity varies with cityscape quality.

Methods

Study system

We worked in 12 community garden sites between 197 and 3656 m² in size, separated by at least 2 km, in Santa Cruz and Monterey Counties in the California central coast in May 2017 (Fig. 1). The gardens in these regions have similar microclimates (i.e., daily max temp and daily average temp) (Lin et al. 2018) but vary in local management of vegetation and groundcover by gardeners, and in their landscape surroundings. All sites are managed towards the cultivation of organic produce, therefore prohibiting the use of pesticides. The sites are surrounded by different amounts of impervious land cover, agriculture land cover (e.g., crop, pasture), and natural land cover (e.g., forest, grass, shrub). We selected the sites because they exist on either a low or high cityscape quality spectrum. We examined cityscape quality within 2 km of gardens because ladybeetles and parasitoids respond positively or negatively to landscape factors (e.g., amount of impervious cover) within this scale in our system suggesting that this spatial scale is important for their movement (Egerer et al. 2017). We examined the surrounding landscape composition with data from the US Geological Survey's 2011 National Land Cover Database (NLCD) (Jin et al. 2013), and calculated the percent impervious land cover (NLCD classes 23, 24; 30 m resolution) within 2 km buffers surrounding the gardens with spatial statistics tools in ArcGIS (v. 10.1) (ESRI 2011). We classified gardens surrounded by > 80% impervious land cover to be low quality cityscapes, and gardens surrounded by < 30% impervious cover to be in high quality cityscapes (Online Resource 1). This resulted in 6 gardens of each landscape type. The difficulty in replicating the experimental treatments across the region (site availability, time) limited our ability to increase treatment replication numbers, and introduces a limitation to our study.

Phase one: floral resource addition experiment

In the first manipulation experiment, we tested whether adding local floral resources affects the abundance, diversity, and composition of ladybeetle and parasitoid communities in gardens of low versus high cityscape quality. We randomly assigned 6 of the

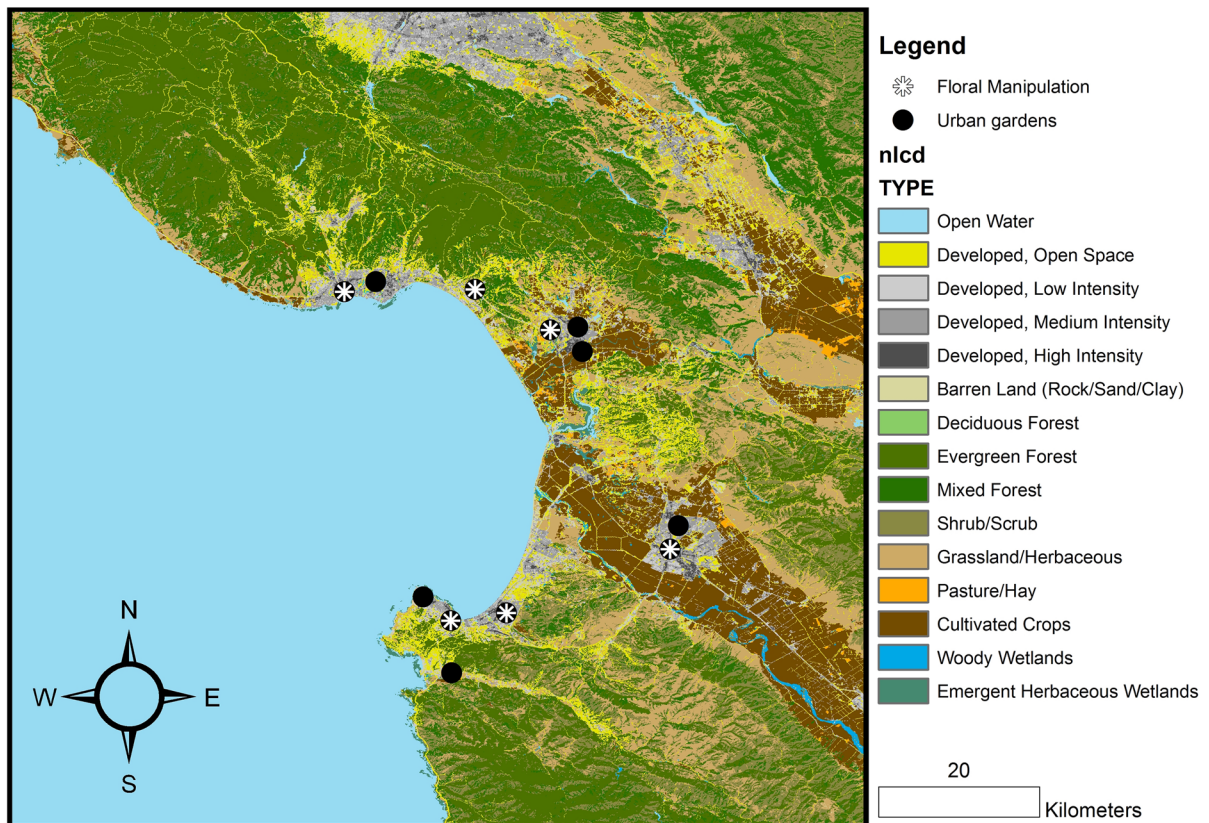


Fig. 1 Urban gardens in the California central coast in which the two-phase study took place. Six of the 12 sites received a floral resource addition (“Floral Manipulation” in legend); all 12 sites received the ladybeetle population manipulation. The

12 gardens (3 in each County, 3 of each cityscape quality) to receive a floral resource addition treatment. This resulted in four treatment groups: (1) gardens in low quality cityscapes with floral resource additions; (2) gardens in high quality cityscapes with floral resource additions; (3) gardens in low quality cityscapes without floral resource additions; and, (4) gardens in high quality cityscapes without floral resource additions. For the floral resource addition, we used three insectary plant species: sweet alyssum (*Lobularia maritima*), common chamomile (*Matricaria recutita*), and cilantro/coriander (*Coriandrum sativum*). These flowering plants are commonly grown in urban and rural agricultural systems to attract and support natural enemies of crop pests, including ladybeetles (Family: *Coccinellidae*), parasitoid wasps (*Apocrita*), and syrphid flies (*Syrphidae*). These arthropods use floral resources at varying life stages for food (nectar, pollen) in addition to the prey that

gardens are surrounded by differences in landscape composition (i.e., land cover classes) classified by the National Land Cover Database (Jin et al. 2013)

they consume or parasitize. All plants were grown under standard conditions in 1 L pots in the Thimann Greenhouse at UC Santa Cruz until flowering.

We assessed the natural enemy community and the floral resource density present in each garden 3 days prior to the floral resource addition (Online Resource 2). To assess natural enemies, we divided each garden into 10×10 m grid sections and placed one yellow $3'' \times 5''$ sticky card trap (Olson Products Inc.) at the center of each section for 48 h. This meant that larger gardens had more traps than smaller gardens in order to account for garden size. We identified all adult ladybeetles to species on the traps. We identified all adult parasitoid wasps to superfamily on the traps, which does introduce a limitation to our biodiversity assessment. In addition, we visually searched for ladybeetle adults on vegetation and groundcover within a 2×2 m area in 8 randomly selected 10×10 m sections in each garden. In smaller gardens

with less than 8 sections (i.e., $> 800 \text{ m}^2$), we randomly selected sections to revisit to visually search in another location within the section. To assess floral density, we established a $20 \times 20 \text{ m}$ survey plot at the center of the garden and counted the number of total flowers in 8 randomly placed $1 \times 1 \text{ m}$ quadrats.

On the day of the floral resource addition, we placed species mixtures of 8 flowering potted plants in each of 5 randomly located $1 \times 1 \text{ m}$ areas for a total of 40 plants within 50 m^2 in each of the six manipulated gardens (Online Resource 1). We added alyssum, cilantro and chamomile in a 2:1:1 species ratio to each garden. Based on floral surveys conducted in each site, we estimate that the floral additions increased floral availability by 1–69% in each site (approximately 1625 flowers were added). We then placed sticky card traps at the center of each $10 \times 10 \text{ m}$ section in each garden. We returned 48 h later to collect the sticky traps, water potted plants, replace wilting plants with fresh pots, and visually survey for ladybeetles at 8 random locations within the garden (8 of the 10×10 grid sections, as above).

Phase two: ladybeetle population manipulation

In the second manipulation experiment, we tested whether difference in cityscape quality and local floral resource addition influences natural enemy site fidelity to gardens using a mark-recapture experiment of a common native ladybeetle species. We released marked individuals of *Hippodamia convergens* in the 12 gardens 4 days after the floral enrichment. *H. convergens* rely on forest cover and vegetation for habitat, disperse $\sim 3 \text{ km}$, consume herbivorous pests like aphids, and are thus popular natural pest control agents used in agriculture. We purchased live adult *H. convergens* from Northwest Beneficials (Bend, OR) prior to the experiment and stored them at $2 \text{ }^\circ\text{C}$ for 5 days following company instructions. For the release, we marked ladybeetles with yellow fluorescent insect marking powder (BioQuip item #1162Y) to identify upon recapture (Online Resource 1). The use of fluorescent powders is a common method in mark-recapture studies to assess dispersal of ladybeetles (Baker et al. 2003), parasitoids (Corbett and Rosenheim 1996), and other insects (Kareiva 1985) because it does not significantly affect survival or flight (Naranjo 1990) and thus recapture. We released 35,000 marked individuals (1/2 US gallon,

recommended amount for small farms and large gardens by these companies (see e.g., www.arbico-organics.com) in each of the 12 gardens during cool ($< 16 \text{ }^\circ\text{C}$) and overcast weather conditions so that ladybeetles could acclimate to and experience the garden.

Prior to releasing the ladybeetles, we measured the density of cabbage aphids (*Brevicoryne brassicae*) in the gardens because a lack of aphid prey resources may also lower the fidelity to gardens. Cabbage aphids feed in dense colonies on *Brassica oleracea* plants (e.g., cabbages, Brussels sprouts, kale), shortening crop life in urban agriculture (Flint 2013), and are the most common aphid species in our system. We visually surveyed live cabbage aphids on 8 randomly chosen *Brassica* plants within the $20 \times 20 \text{ m}$ plot (described above).

We returned to each site after 2, 4, 6 and 12 days following the release to visually survey for marked individuals to assess site fidelity (i.e., the number of individuals that stayed in the garden) as a proxy for dispersal. For the visual surveys, we increased our sampling effort in order to increase recapture probability. We walked along transects corresponding to the garden grids, and stopped every 2–5 m to thoroughly search leaves and groundcover for ladybeetles. We counted all live, marked individuals observed and collected individuals to confirm that they were marked using handheld black lights. Here we assumed that (1) detectability and recapture probability of ladybeetles by researchers was consistent across gardens (we have no reason to believe otherwise), and (2) probability of mortality of ladybeetles over time was consistent across gardens. At the end of the survey we released all counted marked individuals back into the garden. To supplement visual surveys, we placed sticky traps within each of the $10 \times 10 \text{ m}$ grid sections for 48 h (same methods as floral resource addition). We collected all sticky traps and plants 8 days after the release, and did a final visual survey 12 days after the release. This resulted in a total of three sticky trap surveys and four visual surveys. We added the number of ladybeetles on the sticky traps to the prior visual survey for one recapture count for each time point.

Statistical analysis

Effect of cityscape quality and floral resource addition on abundance, richness and community composition

To determine whether cityscape quality and local manipulation affects the abundance and diversity of ladybeetles and parasitoids, we performed two statistical analyses. First, we used generalized linear regression models (GLMs) to compare ladybeetle and parasitoid abundance and richness in gardens in high versus low quality cityscapes before the experiment. This allowed us to test whether cityscapes categorized as high quality support more or fewer natural enemies. We then used GLMs and a model selection approach to measure the relative effect of cityscape quality and floral resource addition on ladybeetle and parasitoid abundance and richness among gardens of the four groups after the manipulation. This analysis was an effort to identify the model structure that best predicted post-experimental ladybeetle and parasitoid abundance and richness considering (1) initial abundance or richness before the manipulation, (2) non-manipulated floral resource density, (3) floral resource manipulation, and (4) cityscape quality. The mean number of individuals and richness of ladybeetle species or parasitoid superfamily observed per trap per site was the response variable. The pre-experimental mean abundance or richness per trap, non-manipulated floral density, landscape type, and floral resource manipulation and their interactions were the predictor variables. We built global models for each response variable using the *glmulti* package (Calcagno and De Mazancourt 2010) and used Akaike's information criterion for small sample sizes (AICc) to determine optimal model structure (Burnham and Anderson 2002). If model AICc values were not different from one another (< 2 points), we averaged the top models to obtain conditional average model coefficients. Analyses were completed in the R statistical environment version 3.2.4 (R Development Core Team 2013).

To determine whether cityscape quality and local manipulation affects the community of ladybeetles and parasitoids, we utilized constrained multivariate analysis – redundancy analysis (RDA) – to measure how much the variation in the composition of natural enemy communities is explained by cityscape quality and floral resource addition. We used a constrained

method because of our a priori hypotheses about the factors that affect composition (i.e., cityscape quality and floral addition). We created a matrix of the variation in species and superfamily composition, and applied a Hellinger transformation using the *vegan* package (Oksanen 2015) in R to standardize abundance across taxa. We used analysis of variance to evaluate the statistical significance of the constraint. To determine whether there were significant differences in ladybeetle and parasitoid community composition in groups before and after the floral resource addition, we used Procrustes analysis using the “protest” function in *vegan* in R to assess similarity among ladybeetle and parasitoid ordinations, respectively. To determine whether there were significant differences in ladybeetle and parasitoid community composition between gardens within groups, we performed an analysis of similarity test (ANOSIM) using the “anosim” function in *vegan* in R.

Effect of cityscape quality and floral resource addition on ladybeetle fidelity to gardens

To determine whether differences in cityscape quality and local manipulation affect the site fidelity of released ladybeetles to gardens over time, we used linear mixed-effects models (LMMs) with repeated measures to model the log transformed number of marked ladybeetles recaptured with site nested within survey time point as nested random effects. We built four models and used AICc for small sample sizes to evaluate model fit: 1) ladybeetle fidelity (recaptures) predicted by cityscape quality; 2) ladybeetle fidelity predicted by cityscape quality and floral resource addition; 3) ladybeetle fidelity predicted by cityscape quality, floral resource addition, and non-manipulated floral resource density; and 4) ladybeetle fidelity predicted by cityscape quality, floral resource addition, non-manipulated floral resource density, and the interaction between floral addition and floral resource density. We did not include garden size as a cofactor in the models because it provided a weaker model fit in the preliminary analysis. Moreover, due to a significant correlation between aphid density and cityscape quality, we included cityscape but not aphid density in the models. We performed a separate LMM with repeated measures to model ladybeetle fidelity predicted by aphid density. LMM analyses were

performed using the *lme4* package in R (Bates et al. 2015).

Results

Effect of cityscape quality and floral resource addition on natural enemy abundance, richness, composition

Floral resource addition had strong impacts on parasitoids – both in abundance and for community composition – but not on ladybeetles. Parasitoid abundance was greater in manipulated gardens than in non-manipulated gardens ($P = 0.009$; Fig. 2c; Table 1) although abundance generally decreased from initial abundance across treatments. We found that the abundance and species richness of ladybeetles and parasitoids were overall relatively greater in gardens in low quality cityscapes than in high quality cityscapes before and after the floral resource addition (Fig. 2), but before experimental differences were not significant (Online Resource 3). Ladybeetle

abundance was lower in gardens in high quality cityscapes than in low quality cityscapes (Fig. 2a), but this was not significant (Table 1). Both ladybeetle richness ($P = 0.02$) and parasitoid richness ($P < 0.02$) were best predicted by greater initial richness before the manipulation and not by floral resource addition or cityscape quality (Table 1).

The floral resource addition significantly changed the composition of parasitoid communities in gardens (Procrustes Sum of Squares (m^2) = 0.47, $P = 0.006$); the gardens with added floral resources were generally more similar to each other in composition, with relatively higher abundance and richness of super-families (e.g., of chalcid and ceraphronid wasps) (Fig. 3d). Cityscape quality explained 7.9% of the variation in the parasitoid ordination before the manipulation, while cityscape quality (9.0%) and the floral resource addition (14.1%) and their interaction (9.7%) together explained a total of 32.7% of the variation in the parasitoid ordination after the manipulation (Table 2). The composition of parasitoid communities did not significantly differ between cityscape types before the manipulation ($F = 1.01$,

Fig. 2 Mean ladybeetle abundance (a), ladybeetle richness (b), parasitoid abundance (c) and parasitoid superfamily richness (d) observed in the 12 gardens of different landscape types before (t_0) and after (t_2) the floral resource addition experiment. Bars show standard error of the mean with 95% confidence interval. *HQC* high quality cityscape, *LQC* low quality cityscape, “+” the addition of floral resources

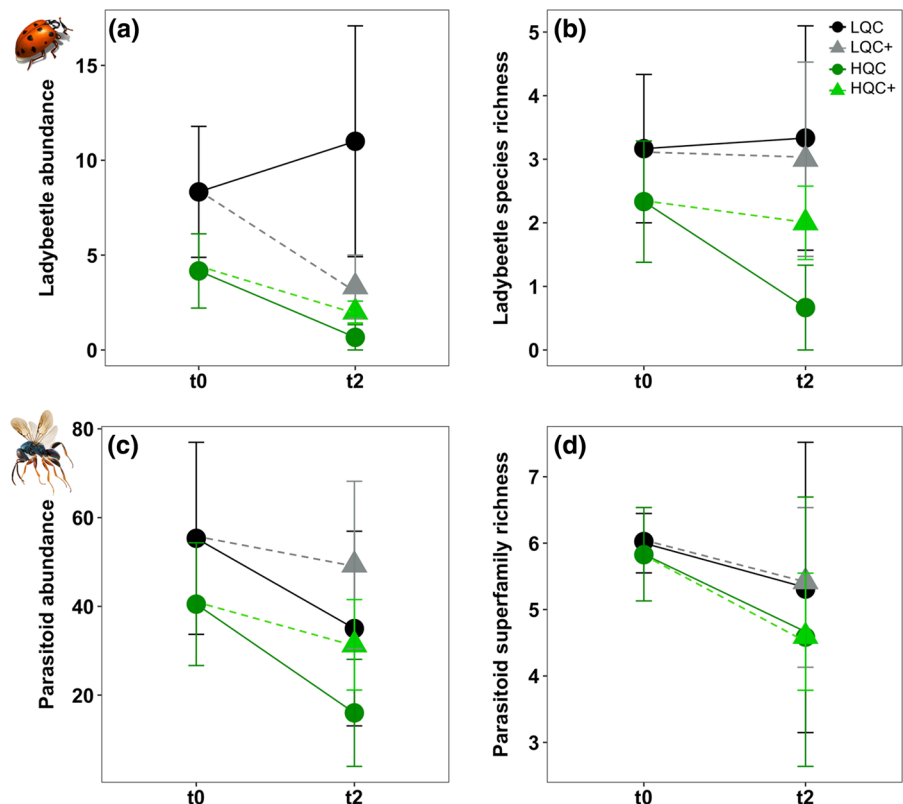
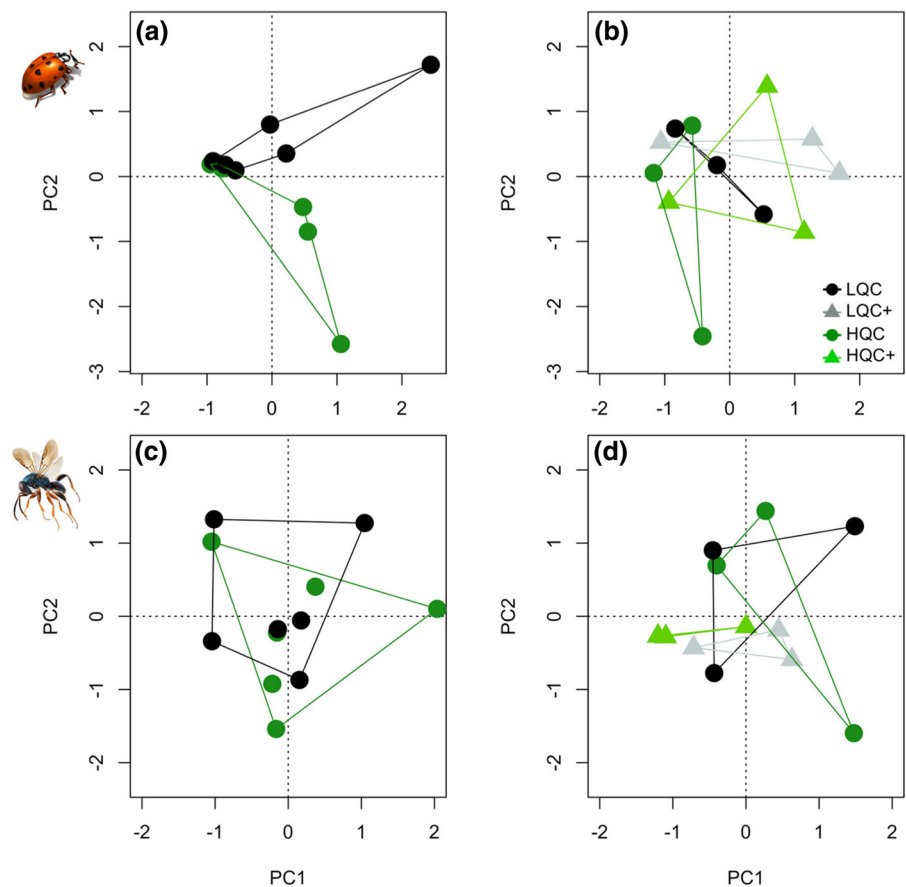


Table 1 Generalized linear models that best predicted parasitoid abundance, parasitoid richness (to superfamily), ladybeetle abundance, and ladybeetle richness (to species) after the floral resource addition where t_0 is the initial abundance or richness before the floral addition

Model	Factor	Coef.	SE _{adj}	z	P	AICc	ΔAICc
Parasitoid abundance	Intercept	0.59	0.82	0.73	0.47	40.73	1.75
	Floral addition (flowers added)	1.52	0.58	2.63	0.009		
	Abundance t_0	0.38	0.22	2.20	0.03		
Parasitoid richness	Intercept	0.02	0.11	0.15	0.89	4.28	0
	Richness t_0	0.71	0.13	5.20	< 0.001		
Ladybeetle abundance	Intercept	0.28	0.13	1.93	0.05	15.74	1.57
	Cityscape (high quality)	- 0.28	0.23	1.22	0.22		
Ladybeetle richness	Richness t_0	0.60	0.21	2.86	0.02	- 16.17	0

Fig. 3 Composition of ladybeetle communities (to species) before (a) and after (b) the floral resource addition experiment in gardens surrounded by two landscape types (HQC high quality cityscape, LQC low quality cityscape) with (“+”) or without the floral resource addition. Composition of parasitoid wasp communities (to superfamily) before (c) and after (d) the floral resource addition experiment



$R^2 = 0.09$, $P = 0.47$; Fig. 3c), nor among groups after the manipulation ($F = 1.28$, $R^2 = 0.32$, $P = 0.26$; Fig. 3d). Parasitoid communities within treatment groups were not significantly different in composition among one another before the manipulation

(ANOSIM: $R = -0.02$, $P = 0.56$), nor within groups after the manipulation ($R = 0.03$, $P = 0.38$). For ladybeetles, cityscape quality explained 9.3% of the variation in the ladybeetle ordination before the manipulation; cityscape (9.2%), the floral resource

Table 2 Results of redundancy analyses (RDA) and subsequent variance partitioning for ladybeetle and parasitoid communities, before and after the floral resource manipulation (i.e., floral resource addition to six gardens)

	Fractions	Variance explained	
		Ladybeetles (%)	Parasitoids (%)
Pre-manipulation	Cityscape	9.3	7.9
	Residuals	90.7	92.1
	Total	9.3	7.9
Post-manipulation	Cityscape	9.2	9
	Floral addition	7.8	14.1
	Cityscape + floral addition	17.02	23
	Cityscape: floral addition	5.08	9.7
	Residuals	77.86	67.3
	Total	22.1	32.7

Rows show the variance explained by pure and joint fractions of cityscape quality (cityscape), floral resource addition (floral addition), unexplained variance (residuals) and total variance explained by all fractions (total)

addition (7.8%) and their interaction (5.1%) together explained a total of 22.1% of the variation in the post-experimental ladybeetle ordination after the manipulation (Table 2). The composition of ladybeetle communities did not significantly differ between cityscape types before the manipulation ($F = 0.43$, $R^2 = 0.04$, $P = 0.81$; Fig. 3a), nor among groups after the manipulation ($F = 0.77$, $R^2 = 0.22$, $P = 0.68$; Fig. 3b). Gardens within groups were not significantly different in ladybeetle community composition before the manipulation ($R = -0.02$, $P = 0.54$), nor within groups after the manipulation ($R = -0.07$, $P = 0.64$). The Procrustes analysis revealed that the manipulation did, however, weakly significantly change ladybeetle community composition ($m^2 = 0.47$, $P = 0.05$). Thus the manipulation had the strongest impact on parasitoid abundance and an effect on ladybeetle community composition, though the total explained variance (22.1% and 32.7%) indicate unexplained variance not accounted for by the explanatory variables.

Effect of cityscape quality and local resources on ladybeetle site fidelity

Landscape type, but not floral resource addition had strong, significant effects on ladybeetle site fidelity to gardens. Gardens in high quality cityscapes had significantly higher recaptures of marked ladybeetles over time than gardens in low quality cityscapes ($P < 0.001$; Fig. 4), and the optimal model structure

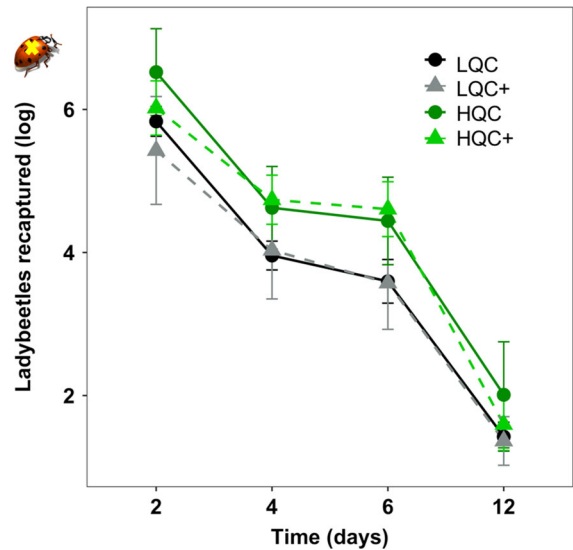


Fig. 4 Site fidelity – the number of marked ladybeetles recaptured (log transformed) – to gardens surrounded by two landscape types (*HQC* high quality cityscape, *LQC* low quality cityscape) with (“+”) or without the floral resource addition over the study period. Bars represent the standard error of the mean with 95% confidence interval

predicting site fidelity only included cityscape type (Table 3). Counter to our expectations, the floral resource addition did not significantly affect this pattern, nor did the floral density already present (Table 3). Aphid density did not significantly directly affect marked ladybeetle recaptures ($P = 0.75$; Table 3); however, aphid density was significantly

Table 3 Linear mixed models (A-E) predicting ladybeetle site fidelity to gardens by cityscape quality (cityscape), floral resource addition (floral addition), and non-manipulated floral resources present (floral density) in gardens

Model	AICc	Factor	Coef.	SE	t	P
A. Site fidelity ~ cityscape	136	Intercept	3.65	0.80	4.55	< 0.001
		Cityscape (high quality)	0.67	0.22	3.00	0.004
B. Site fidelity ~ cityscape + floral addition	139	Intercept	3.72	0.82	4.54	< 0.001
		Cityscape (high quality)	0.67	0.22	2.98	0.005
		Floral addition	- 0.13	0.22	- 0.59	0.56
C. Site fidelity ~ cityscape + floral addition + floral density	140	Intercept	3.84	0.86	4.47	< 0.001
		Cityscape (high quality)	0.71	0.24	2.98	0.005
		Floral addition	- 0.09	0.24	- 0.35	0.73
		Floral density	- 0.05	0.10	- 0.54	0.59
D. Site fidelity ~ cityscape + floral addition × floral density	141	Intercept	3.18	0.93	3.41	0.002
		Cityscape (high quality)	1.02	0.28	3.63	< 0.001
		Floral addition	1.30	0.75	1.73	0.09
		Floral density	0.13	0.14	0.98	0.33
		Floral addition: floral density	- 0.43	0.22	- 1.94	0.06
E. Site fidelity ~ aphid density	183	Intercept	3.79	0.82	4.60	< 0.001
		Cabbage aphid density	0.11	0.32	0.33	0.75

Fidelity was measured as the number of marked ladybeetles recaptured (log transformed) after the experimental release. Day of sampling nested within garden site are random effects. Interactions between terms are represented by ×

higher in low quality cityscapes (Welch Two Sample *t* test; $t = -5.4$; $P < 0.001$; Online Resource 4).

Discussion

Cityscape quality influences the fidelity of natural enemies (ladybeetles) to urban gardens, and more so than local resource availability. However, increasing floral resources through floral resource addition increases the abundance of and changes the composition of other natural enemy (parasitoid) communities in urban gardens, which may increase pest control services. We found lower site fidelity of marked ladybeetles to gardens in low quality cityscapes (those surrounded by more impervious land cover). We also found that gardens in low quality cityscapes maintained relatively higher ladybeetle and parasitoid abundance and richness compared to high quality cityscapes (those with less impervious cover and more mixed land use) throughout the experiment. Our results show that natural enemies disperse more quickly from habitat patches in low quality cityscapes,

and that these habitat patches have abundant and diverse natural enemy communities. The results suggest that natural enemies may move relatively fast in more impervious surroundings, colonizing relatively high quality habitat patches quickly, but have low fidelity to these habitats. Habitats in low quality cityscapes may therefore have relatively high turnover of individuals and maintain high diversity.

The built environment is less conducive to site faithfulness than we hypothesized. Under the framework of agricultural landscape theory, we hypothesized that agroecosystems in cityscapes with more natural cover were of higher quality for natural enemies and that they would better support biodiversity, facilitate dispersal due to landscape connectedness, and therefore would have lower site fidelity to a garden. Indeed, presence and quality of natural habitat in the landscape both facilitates dispersal and supports higher species richness of natural enemies in agricultural landscapes (Gardiner et al. 2009). Our results show that cityscape effects on natural enemy communities and dispersal differ from the rural context. Drawing from diffusion theory, which predicts lower

population densities in land cover that facilitates movement (Schultz et al. 2017), it seems that in our system impervious cover and associated features of the urban environment favor site infidelity of individuals to the garden system. Many (possibly most) organisms move faster in the landscape matrix than in habitat patches (Kareiva and Odell 1987; Schultz 1998; Brown et al. 2017; Lutscher and Musgrave 2017), attributed in part to edge effects. In low quality cityscapes with greater impervious habitat, individuals are more likely to come upon an edge, thereby triggering long range movement to the next high quality patch. Yet in gardens that are in higher quality cityscapes, there may be less of a difference in habitat quality between the garden and the surrounding cityscape, meaning that organisms are more likely to experience an edge less frequently and are thus less likely to undertake large movements. In other words, ladybeetles that leave a habitat patch (e.g., a garden) in a low quality cityscape might move away from the area more frequently or might not find the patch again due to higher flight response. Furthermore, the associated features of urban environments such as thermal, light and noise pollution can also affect insect populations and behavior (McIntyre 2000). Indeed, prolonged warmer temperatures and increased artificial illumination may disorient individuals, extend foraging time, and increase dispersal likelihood (Longcore and Rich 2004) and thereby site infidelity.

Local agroecosystem habitat management variably affects natural enemies. The floral resource manipulation supported greater parasitoid abundance and changed community composition, though abundance and richness were lower after the manipulation. The later result may be due to the removal of individuals from the population with sticky traps, and because individuals were less dispersed in the garden (which our sampling method favored) and more concentrated at the introduced plants. The manipulation had no effect on ladybeetle communities or fidelity, which is surprising because we have found floral abundance to be an important predictor of ladybeetle abundance across sites, particularly in gardens surrounded by more natural land cover (Egerer et al. 2016), and because we observed marked ladybeetles utilizing the plants in the gardens during the study. Given that the floral resource additions only increased floral abundance by less than 10% in some gardens, this may not be enough to trigger differences in ladybeetle site

fidelity or movement to or from a garden. However, even small additions of flowers can support greater parasitoid populations, which are sensitive to floral presence in urban habitats (Bennett and Gratton 2012) likely due to the importance of floral nectar for their life history (Ellis et al. 2005; Balzan and Wäckers 2013). Urban gardeners can thus provision for natural enemies like parasitoids and therefore natural pest control with the simple addition of flowering crops that are utilized by both people and insects.

Gardens in low quality cityscapes had significantly more aphid herbivore food resources, but aphid density did not significantly directly affect ladybeetle fidelity to gardens. In urban gardens, plant nutrient and water availability are usually heavily supplemented, thereby reducing resource limitation for herbivores (Raupp et al. 2010), and potentially reducing the effectiveness of natural enemies to control them. Urbanization processes may change the strength and importance of direct and indirect effects on trophic interactions between natural enemy and herbivore (Shrewsbury and Raupp 2000), thus it is still possible that aphid density contributes to the effect of cityscape quality on ladybeetle dispersal through indirect effects. Furthermore, the methodological nature of the study assumed that ladybeetle mortality was similar in gardens between landscape types. Yet cityscape quality might also affect ladybeetle predator abundance, such as spiders, thereby affecting ladybeetle mortality and site fidelity. We observed few instances of marked ladybeetle predation by wolf spiders (Lycosidae), which are more active and diverse in gardens with greater floral abundance and in gardens surrounded by agriculture, but not impervious land cover (Otoshi et al. 2015). Moreover, most ladybeetle mortality from predation occurs at the egg or larval rather than adult stage (Weber and Lundgren 2009). Thus while differences in predation in gardens of different cityscape quality could affect ladybeetle site fidelity, we do not have strong evidence of ladybeetle predation effects driving our results.

Urban gardeners are in need of more information on how to sustainably manage pests, as community gardens often require organic practices that prohibit the use of pesticides (Oberholtzer et al. 2014). Although we did not directly test the effects of site fidelity on pest removal, our results may suggest that gardeners at high fidelity sites may benefit from greater pest control services if ladybeetles consume

more pests during their longer residency. On the other hand, gardeners at low fidelity sites in low quality landscapes may have lower pest control by ladybeetles in addition to having higher pest abundance. We cannot definitively link fidelity to greater pest control services, but we can suggest that gardeners in these sites may augment their plots through addition of flowering plants to support parasitoids to potentially increase pest control. Future work that assesses how food web relationships among herbivore pests and natural enemies change in strength and direction with differences in landscape type and local resource availability may impart further insight into management application.

We continue to unravel the mechanisms driving natural enemy community ecology and population dynamics in this system. Our previous work suggested that gardens in high quality cityscapes with greater local resource availability may relax dispersal processes and increase the site fidelity of natural enemies to gardens, while gardens in low quality cityscapes may accumulate species due to high colonization and low dispersal (Egerer et al. 2016). While our first conclusion seems to stand with this presented work, our second conclusion requires reconsideration. Gardens in low quality cityscapes may have high biodiversity, colonization, and site infidelity of natural enemies to suggest that urban agroecosystems have more dynamic, rather than static, populations than previously thought.

Conclusion

The landscape matrix is increasingly recognized as a vital resource for biodiversity (Ricketts 2001) and for supporting ecosystem services provided by mobile organisms (Perfecto and Vandermeer 2002; Schellhorn et al. 2015b). Landscape matrix quality can promote or hinder population movement, habitat colonization, and local and regional extinction probability (Vandermeer and Carvajal 2001). Theory predicts that higher quality landscapes generally beget higher biodiversity maintenance by providing resources over space and time to mobile agents (Kremen et al. 2007). Yet, in low quality cityscapes of high impervious land cover, associated abiotic disturbances, and patchy resource availability, population movement and the site fidelity of organisms to

urban habitat patches can change. Using natural enemies in community gardens as a model system, we show how site fidelity in the cityscape matrix may follow a different paradigm. Although gardens within lower quality cityscapes had lower ladybeetle fidelity to them, the maintenance of natural enemy diversity within these agroecosystems surrounded by high impervious land cover may further suggest that urban habitat patches are connected through species dispersal. Therefore, it is important to preserve greenspaces like urban gardens for biodiversity conservation in cityscapes.

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Author contributions MHE, SMP and HL conceived of the study and designed the field experiments. MHE, SMP, HL, and PB carried out the field experiments. MHE conducted statistical analyses and wrote the first draft of the manuscript. All authors improved the manuscript.

Compliance with ethical standards

Conflicts of interests The authors declare that they have no conflict of interest.

Data accessibility Data have been made available in the supporting documents.

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