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RESEARCH

Agricultural management and landscape drivers of arthropods associated with *Cucurbita pepo* in urban agroecosystems

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Abstract

Agricultural habitat and landscape factors influence arthropod community structure in urban agroecosystems, thereby influencing the crucial role that arthropods play in supporting ecosystem services, such as biological pest control. Top-down regulation can be enhanced or diminished by shifts in arthropod communities, thus, understanding which factors alter abundance and richness of herbivores and natural enemies in agroecosystems can guide approaches to habitat management and pest control strategies. We examined which local habitat factors (e.g., ground cover, floral abundance, vegetation height) and landscape factors (e.g., urban cover) drive changes in herbivore and natural enemy abundance, richness, and composition on squash (*Cucurbita pepo*) plants in urban agroecosystems. We collected and identified arthropods from foliage, stems, and flowers using visual surveys on *C. pepo* plants across 21 urban agroecosystems in the central coast of California. Both local and landscape factors were associated with shifts in abundance and richness of specific herbivore and natural enemy taxa. Specifically, squash area was associated with higher abundance of leaf beetles and herbivore Hemiptera and herbaceous plant richness tended to predict lower herbivore, aphid and leaf beetle abundance. Squash area was associated with higher natural enemy abundance and richness, higher spider and ladybeetle richness, and higher predator Hemiptera abundance. Garden size boosted natural enemy and ladybeetle abundance and ladybeetle richness. Tree and shrub abundance was associated with higher spider, ladybeetle, and predator Hempitera abundance. Herbaceous plant richness was associated with lower ladybeetle abundance and richness. Finally, urban cover boosted predator Hemiptera abundance and richness. No local or landscape factors predicted shifts in herbivore or natural enemy composition. We examine why and how specific local and landscape habitat factors shape the arthropod community structure in a common garden crop and consider implications for garden management practices.

Keywords Agroecology · Biodiversity · Conservation biological control · Garden · Herbivore · Natural enemies · Squash

Introduction

Insects and spiders, two important groups of arthropods, are critical components of agroecosystems, and depending on their functional role can impact plant growth, disease transmission, herbivore regulation, and delivery of ecosystem services. Agroecosystem management and landscape intensification can impact the abundance and diversity of beneficial arthropods (Philpott et al. 2020a), but impacts may depend on specific local habitat features (Burks and Philpott 2017; Philpott and Bichier 2017), arthropod taxon (Raupp et al. 2010), as well as the crop species examined (Ploessl et al. 2023). Thus, understanding how management influences ecosystem services, such as biological control of herbivorous insects, is context dependent. Conservation biological control approaches identify and evaluate how habitat management efforts can enhance the regulation of herbivores through various ecological interactions (i.e., predation, parasitism, facilitation) (Barbosa 1998; Rusch et al. 2017). While traditional conservation biological control

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research has mostly taken place in rural agricultural contexts, the rise of fragmented and urbanized landscapes has propelled research in urban ecosystems, including urban agroecosystems (Alberti et al. 2003; McIntyre 2000; Raupp et al. 2010).

Conservation biological control approaches in urban agroecosystems that account for the multifunctionality of urban agriculture and the unique features of the urban matrix can support both biodiversity and people (Jha et al. 2023; Lin et al. 2015). Urban agroecosystems can increase genetic diversity through crop selection, improve local climate and air quality, and increase soil fertility and water holding capacity (Egerer et al. 2018; Evans et al. 2022). For example, urban agriculture systems can provide food resources for populations of insectivorous bats, birds, and mammals, as well as herbivore regulation for plant protection (Aguiar et al. 2021). Ecosystem services, such as predation and pollination, are provided by insects and spiders and the extent of services provided can vary depending on vegetation structure and complexity and resource connectivity across the landscape (Di Pietro et al. 2018; Lucatero et al. 2024). Projected urban growth suggests that 68% of the world's population could reside in urbanized areas by 2050; if this projection materializes then the value and contributions of urban agriculture can become fundamental for local food production systems (United Nations 2019).

Arthropods, like other organisms, rely on resources distributed across landscapes composed of unique habitats with different ecological features (Rand et al. 2006). Both local and landscape features thus impact insect and spider communities. A focus on plant diversity and structure first guided analyses of herbivores and natural enemy community structure (Andow 1991; Risch 1981) where on-the-farm (local habitat) factors (i.e., canopy cover, monoculture vs. polyculture designs) were considered the primary drivers of agroecosystem impacts. In urban gardens specifically, several urban agroecosystem features and disturbances influence arthropod abundance and diversity. For instance, in rural agroecosystems, higher host plant density is often linked to higher herbivore abundance as described in the 'resource concentration hypothesis' (Risch 1981; Root 1973). Garden management strategies like crop rotations or repetitive planting can result in patch-size outbreaks of herbivorous insects and shift abundances (Taylor et al. 2017). Yet, several studies fail to document impacts of local management factors on herbivore abundance and richness potentially because local factors are influencing other aspects of herbivore communities (e.g., feeding guilds, composition) or due to low sample effort (Lowenstein and Minor 2018; Lucatero et al. 2024). A different suite of habitat and landscape factors may shape natural enemy communities and also differ depending on taxa. For instance, the activity density of generalist predators (i.e., spiders, ants, and beetles) sometimes, but not always, shifts depending on urban habitat type (i.e., forest, urban, vacant lots) and habitat features (i.e., mulch, grass, shrubs) (Burkman and Gardiner 2014; Philpott et al. 2014). Spider species richness is higher in gardens with more mulch, flowering vegetation, and trees (Lowe et al. 2018; Otoshi et al. 2015). Ant species diversity can be reduced by disturbance in gardens (i.e., tillage intensity, clay or wet soils); however, ant species respond differentially to grass and wooded areas potentially due to different life-history strategies (Edwards 2016). Ladybeetles express sensitivity to mulch but can benefit from garden features that create habitat complexity (i.e., ornamental plant richness, shrubs, trees, and flowering plants) (Egerer et al. 2017b). Parasitoid abundance can be shaped by floral resources (Egerer et al. 2018a) or by hyperparasitism, dispersal, and habitat fragmentation (Arnold 2022). Thus, overall, herbivore and natural enemy groups vary in their responses to garden-based (local) factors, highlighting the complexity of understanding the specific habitat requirements among arthropod groups.

Arthropod communities also respond to temporal and spatial shifts across entire landscapes, as highlighted by studies of both metapopulation biology and landscape ecology (e.g., Levins 1969; Vandermeer and Carvajal 2001). For example, incorporating non-crop resources outside of cultivated crops (e.g., flower field strips, weeds, and grasses), and shifting landscape composition (e.g., increases in semi-natural habitat, native vegetation) can support arthropod abundance and diversity (Tscharntke et al. 2005). Non-crop resources can provide sites for reproduction, prey items, and support dispersal (Bianchi et al. 2006). Ladybeetles, for example, can seek refuge in urban gardens surrounded by low amounts of natural cover (i.e., forests) (Egerer et al. 2018a); whereas impervious cover (i.e., vacant parking lots) can dampen the positive effect of urban gardens (Parker et al. 2020). Other natural enemies, like parasitoids, are susceptible to urban cover, and this often results in decreased species richness (Bennett and Gratton 2012; Burks and Philpott 2017), suggesting that urbanization can act as a filter on specialized feeding strategies (Rocha and Fellowes 2020). More recent studies demonstrate that landscape context mediates the responses of arthropods to local management features (Jha et al. 2023) as well as the importance of 'hidden' temporal and spatial heterogeneity across rural landscapes (Vasseur et al. 2013). Thus, including both local and landscape components is necessary to understand arthropod responses to agroecosystem change. Given the cultural significance and preference for specific food crops, learning if arthropod communities express crop-specific differences across different local and landscape features remains vital.

In this study, we considered arthropods foraging on a common urban agroecosystem crop, squash (*Cucurbita*

pepo). We selected squash because it is grown in nearly all urban agroecosystems in the study region, and has high cultural significance for many gardeners. Use of a focal crop to study arthropods is a common technique that has been employed in other studies of urban agroecosystems (e.g., brassica crops in Lowenstein and Minor 2018; Philpott et al. 2020b). Squash which includes zucchini, summer squash, acorn squash, and pumpkins, is a food crop and companion plant of the milpa or three sisters corn-bean-squash polyculture system grown in Native communities across the Americas (Kimmerer 2013; Lira et al. 2016). Squash is also cultivated for commercial purposes throughout North America and has become a model crop for studies on pollination biology (Knapp and Osborne 2019; López-Uribe et al. 2016), analyses of mechanisms of resistance to plant herbivores (Brzozowski et al. 2019), and pest regulation associated with farm management (i.e., organic, polyculture vs. monoculture) (Mabin et al. 2020). For example, polyphagous herbivores like cucumber beetles (*Diabrotica undecimpunctata* and *Acalymnna vittatum*) form a pest complex that expresses unique group behavior and interactions with semiochemicals released by male individuals (Haber et al. 2021; Rojas et al. 2015). Herbivores like *Anasa tristis* express ovipositional preferences in specific cucurbit varieties (Cornelius et al. 2019). Aphids and whiteflies can incur various types of plant damage, including vectoring diseases like the Zucchini Yellow Mosaic Virus and Cucumber Mosaic Virus (Nyoike and Liburd 2010) and contribute to Cucurbit Leaf Crumple Virus (Akad et al. 2008). In rural farm contexts, insectary plants have been added to pumpkin farms to measure the predation of herbivore species eggs (Phillips and Gardiner 2016) and some research has considered natural enemy responses to mulch and intercropping with *C. pepo* (Athey et al. 2022; Hooks et al. 1998). Thus, *C. pepo* is an excellent crop to understand how arthropod communities impact crop health, food production, and herbivore regulation.

While many studies have investigated how farm management practices (e.g., tillage, cover crops, flower strips) influence the abundance of natural enemies on *C. pepo* in commercial farms (Appenfeller et al. 2022; Cornelius et al. 2019; Lopez and Liburd 2022; Phillips and Gardiner 2016; Skidmore et al. 2019), little work investigates management or landscape influences on *C. pepo* arthropods in urban gardens. In urban agroecosystems, research on *C. pepo* arthropods is limited to examining *C. pepo* damage associated with fungivorous Coccinellidae (Egerer et al. 2020) or arthropod surveys of gardens that include *C. pepo* as one of many plant species (Gregory et al. 2016; Ploessl et al. 2023). In our study, we asked how arthropods found on *C. pepo* plants in urban agroecosystems respond to both local garden management practices as well as changes to the landscape surroundings. Our specific research questions were: (1) How do local garden management practices and landscape factors impact the abundance and richness of herbivores associated with *C. pepo*? (2) How do local garden management practices and landscape factors impact the abundance and richness of natural enemies (predators and parasitoids) associated with *C. pepo*? (3) How do local garden management practices and landscape factors impact specific herbivore and natural enemy taxa?, and (4) How do local garden management practices and landscape factors impact herbivore and natural enemy species composition? Given that herbivores typically respond to the availability of their preferred host crop (e.g., Rhainds and English-Loeb 2003), we predicted that herbivore abundance would increase with the *C. pepo* density in gardens. Given that parasitoids and predators often respond to both impervious cover and floral resources, we predicted that floral resources would increase both the richness and abundance of parasitoids and predators, and that abundance and richness of natural enemies would decrease with increases in impervious cover.

Methods

Study system

We worked in 21 urban agroecosystems (i.e., community gardens where vegetables, fruits, and ornamental plants are cultivated) in the summer of 2021 across three counties (Monterey, Santa Clara, and Santa Cruz) in the Central Coast region of California (Table S1). Most of the study gardens consist of many plots each managed by individual gardeners, but a few reflect the decisions of a single employee or manager. We selected gardens that were surrounded by differing amounts of natural, urban, and agricultural cover and that were located at least 2 km away from each other garden (Table S1). The gardens had been cultivated for between 5 and 47 years and were between 1,000 and 20,000 m in size. We visited each site once between June 21–25 and once between August 9–13.

Arthropod surveys and identification

In each garden, we sampled arthropods by haphazardly selecting up to 10 *C. pepo* plants within a 20 m x 20 m plot in June and a different set of 10 haphazardly selected plants in August for a total of 20 plants surveyed in each site. We visually inspected each *C. pepo* plant for approximately 10 min, searching all above ground plant parts (e.g., leaves, stems, flowers), and collected each arthropod that we could not identify to species in the field in vials with 95% ethanol.

On the same days that we sampled for arthropods, we also measured the height and width of each *C. pepo* plant sampled, calculated the area for each plant following the formula for the area of a tringle, and summed the total plant area sampled in each garden. In one site, we surveyed 19 instead of 20 *C. pepo* plants across the two sample periods because there were only 9 plants in our study plot in June. Nevertheless, the total plant area surveyed in this site was near the mean value of total *C. pepo* area sampled across all sites (Table S1).

We identified all arthropods to order, family, genus, and species or morphospecies using identification keys and guides (e.g., Borror and White 1970; Fisher and Cover 2007; Marshall 2006) as well as online resources (BugGuide 2022; Spencer Entomological Collection 2021; UC IPM 2021; UF IFAS 2021, and collections stored in the Philpott Lab at UC Santa Cruz). We classified each arthropod to life stage (adult, larva, nymph, pupa, and egg). We also categorized all arthropods to feeding group (i.e., herbivores, predators, parasitoids, decomposers, nectarivores) following information available in the identification guides and keys. For data analysis, we only considered feeding life stages (adults, larvae, and nymphs) and only used information for the herbivores, predators, and parasitoids, the latter two of which were combined as the natural enemies group.

Local, garden management factors

To understand how urban garden habitat management may be impacting arthropods associated with *C. pepo*, we measured several local factors that are documented drivers of arthropod communities in urban agroecosystems (e.g., Philpott et al. 2014). We noted garden age, measured the size of each garden, as well as the mean plot size in each garden. We established a 20 m x 20 m plot at the center of each garden, within which we sampled various vegetation and ground cover features. We counted the total number of trees and shrubs, number of tree and shrub species, and the number of trees and shrubs in flower. Within the 20 × 20 m plot, we randomly selected eight 1 m x 1 m plots within which we measured the height of the tallest herbaceous vegetation and estimated the percent cover from bare ground, mulch or wood chips, straw, leaf litter, grass, rocks, and herbaceous plants. We also estimated the percent ground cover from each plant species, which we used to compile plant species richness for each site. We also counted the number of flowers for each plant species in each plot. For both simple and compound flowers, we counted each visible flower. For plants with many inflorescences, we counted individual flowers on each of five inflorescences and multiplied the average number of flowers per inflorescence by the number of total visible inflorescences to estimate total floral abundance on a plant.

Landscape factors

We calculated the percentages of different land cover classes within 2 km buffers from the center of each garden. We selected a spatial radius of 2 km for all land cover classifications as previous studies in these sites found this an appropriate scale to measure landscape impacts on the abundance and richness of most arthropod groups (Egerer et al. 2017a; Philpott et al. 2025). To do this, we used land-cover data from the 2019 National Land Cover Database (NLCD, 30 m resolution) (Homer et al. 2015). We used the 'landscapemetrics' package (Hesselbarth et al. 2019) in R (Core Team 2023) to calculate the percent of each NLCD land-cover class within a 2 km buffer from the center of each garden. With the NLCD land-cover class information, we created four land-cover categories: 1) natural (including NLCD categories of deciduous, evergreen, and mixed forests, dwarf scrub, shrub/ scrub, and grassland/ herbaceous); 2) open (including lawn, park, and golf courses); 3) urban (including low, medium, and high intensity developed land); and 4) agriculture (including pasture/ hay and cultivated crops). Other land-cover classes covered < 5% of the surrounding landscape and were not included in our analysis.

Data analysis

We calculated the total abundance and species richness of herbivores and natural enemies for each site, pooling data from all *C. pepo* plants sampled across both sample dates. We also calculated the abundance and richness of common taxonomic groups defined as any herbivore or natural enemy taxon collected from at least 50 individuals across all sites. For herbivores, we examined the abundance of all herbivores, aphids, whiteflies, leaf beetles (Chrysomelidae), and herbivore Hemiptera (not including aphids and whiteflies). Because aphids and whiteflies were highly abundant compared to any other herbivore group, we also examined total herbivore abundance excluding those two groups. For species richness, we examined all herbivores, leaf beetles, and herbivore Hemiptera (not including aphids and whiteflies). For natural enemies, we examined abundance and species richness of all natural enemies, parasitoid wasps, ants, spiders, predatory Hemiptera, and ladybeetles (Coccinellidae). Instead of examining raw species richness, we consider here estimated species richness (Chao1) that we calculated using the 'vegan' package in R (Oksanen et al. 2013). We used estimated species richness for two reasons. First, we used estimated species richness in case we had under sampled any particular arthropod taxa in a site. Second, qualitative

model outputs for raw species richness values were similar to model outputs for estimated species richness, and we just report one value for brevity. Our next step was to choose which local and landscape factors to include as predictor variables in our statistical models. We first tested for correlations between groups of predictor variables using Pearson correlations tests with the 'corrplot' (Wei and Simko 2024), 'Hmisc' (Harrell 2025), and 'Performance Analytics' (Peterson and Carl 2024) packages in R. We grouped predictor variables into four categories: (1) general garden factors including garden age, garden size, and plot size; (2) ground cover factors including bare ground, mulch or wood chips, straw, leaf litter, grass, rocks, and herbaceous plants; 3) vegetation factors including vegetation height, herbaceous plant richness, flowering herbaceous plant richness, number of flowers, number of trees and shrubs, and number of trees and shrubs in flower; and (4) landscape factors including open cover, natural cover, agricultural cover, or urban cover each within 2 km of the garden. Garden size was significantly correlated with garden age (correlation coefficient = 0.92) and with plot size (0.48). Thus, we chose to include garden size in our models. Rocks and straw cover were low (less than 5% on average), and we did not include those variables in our tests. Bare ground was correlated with mulch cover (-0.62), and leaf litter was correlated with herbaceous cover (-0.46), thus we included bare ground, leaf litter, and grass in our initial models. Herbaceous plant richness was correlated with flowering herbaceous plant richness (0.93), the number of trees and shrubs was correlated with the number of tree and shrub species (0.72), so we initially included vegetation height, herbaceous plant richness, number of flowers, and number of trees and shrubs in models. Finally, urban cover was correlated with natural cover (-0.80) and open cover (-0.62), and agriculture covered only about 6% of the landscapes on average, so we only included urban cover in our models. We also included the total area of squash plants sampled across both sample periods. We tested all selected variables for multicollinearity. We used the variable inflation factor (VIF) using the 'car' package in R (Fox and Weisberg 2018) and removed any predictor variables with VIF scores higher than 2. Thus, the final list of predictor variables included garden size, squash area sampled, vegetation height, herbaceous plant species richness, number of trees and shrubs, bare ground cover, and urban cover within 2km. We used natural log transformed values for garden size and squash area sampled, and square root transformed values for the percent of urban cover in all analyses.

We used generalized linear models (GLM) to test for significant relationships between the predictor variables and abundance and estimated species richness (Chao1) of herbivores, natural enemies, and select herbivore and natural enemy taxa. Specifically, we used the dredge function in the 'MuMin' package in R (Barton 2012) to evaluate the impact of the predictor variables described above using multimodel inference. The package generates top models based on Akaike Information Criterion (AIC_c) values. For any model where the top model was not separated from other models by >2 AIC_c points, we averaged all of the models where the AIC_c was within two points of the next best model with the *model.ave* function in the 'MuMin' package in R. We derived our z and p values from the conditional average of the summary of our GLM models.

In order to choose the best error structure for each model, we compared Akaike Information Criterion (AIC_c) scores for several error distributions for each variable (Table S2, Table S3). We also used the 'Dharma' package in R (Hartig and Hartig 2022) to plot QQ and standardized residuals to visually assess model fits, to test for overdispersion, and to check for quantile deviations. For each abundance variable, we ran GLMs with Gaussian, negative binomial, and Poisson error distributions for both raw values and log-transformed values. For each estimated species richness variable, we ran GLMs with Gaussian and negative binomial distributions for raw data, and one case used a Gamma distribution for raw data and in another case a Gaussian distribution for log-transformed data (Table S3). We used untransformed variables and the error distribution with the lowest AICc score if this did not violate DHARMa tests, and selected the transformed variable and error structure with the lowest AIC score if any DHARMa tests indicated significant overdispersion or quantile deviations. For abundance data, we used raw data for the numbers of leaf beetles, parasitoids, spiders, ants, and ladybeetles and log-transformed data for numbers of herbivores, other herbivores (excluding aphids and whiteflies), aphids, whiteflies, herbivore Hemiptera, natural enemies, and predator Hemiptera (Table S3, Table S4). We used raw data for all estimated richness values except for the use of log-transformed data for the number of predator Hemiptera species (Table S2, Table S3). We used a negative binomial distribution for numbers of leaf beetles, parasitoids, parasitoid species, spiders, spider species, ants, ladybeetle species, a Poisson distribution for number of ladybeetles, a Gamma distribution for natural enemy species, and a Gaussian distribution for all other variables (Table S2, Table S3). Although we are aware of pitfalls associated with variable transformations (e.g., O'Hara and Kotze 2010), in our case, using raw variables, in several cases, provided much poorer model fit and significant quantile deviations (Table S2, Table S3).

We examined the residuals of all models for the 21 dependent variables for spatial autocorrelation with the 'ape' package in R (Paradis 2012). There was no evidence

of significant spatial autocorrelation for any variable (Table S4).

To examine differences in herbivore and natural enemy composition in sites with different local management factors and landscape composition, we used two methods. First, for herbivores and then for natural enemies, we ran two permutational multivariate analysis of variance (PERMANOVA) tests using the *adonis2* function in the 'vegan' package (Oksanen et al. 2013) to determine if garden size, squash area sampled, vegetation height, herbaceous plant species richness, number of trees and shrubs, bare ground cover, or urban cover within 2 km were predictive of herbivore or natural enemy species dissimilarity. We used abundance values for herbivores and natural enemies for this analysis. We used Bray-Curtis distances and conducted 999 permutations for each community. Next, we created nonmetric multidimensional scaling (NMDS) plots in 'ggplot2' (Wickham 2016) to visualize differences in composition between sites, and added arrows for predictors of herbivore or natural enemy species composition to plots using the *envfit* function in the 'vegan' package (Oksanen et al. 2013).

We conducted all statistical analyses in R version 4.1.3 (R Core Team 2023).

Results

We identified 17,650 herbivore and predator arthropods across all sites sampled, including a total of 20 herbivore families from 38 species or morphospecies and 40 natural enemy families from 126 species or morphospecies. The most common herbivores that we found were aphids (13,505 individuals), whiteflies (488 individuals), leaf beetles (Chrysomelidae, 107 individuals), and leaf hoppers (Cicadellidae, 49 individuals) (Table S5). The most common natural enemies encountered were ants (2,488 individuals), spiders (255 individuals), flower bugs (Anthocoridae, 75 individuals), and ladybeetles (Coccinellidae, 60 individuals) (Table S6).

Overall, the selected local and landscape factors had no significant influence on herbivore abundance or estimated species richness in gardens. While the abundance of herbivores, aphids, and leaf beetles tended to decline with increases in herbaceous plant species, and abundance of leaf beetles and herbivore Hemiptera tended to increase with area of squash sampled in a garden, there were no local or landscape variables that significantly predicted the abundance of any herbivore (Table S7). Likewise, no local or landscape factors significantly predicted the estimated species richness of herbivores overall or for any individual herbivore group (Table S7).

For natural enemies, both local and landscape factors were associated with changes in abundance and richness for all natural enemies and for specific taxa of natural enemies (Table S8). We found higher abundance of natural enemies in larger gardens ($p=0.044$, Fig. 1A) and higher natural enemy richness in gardens with more squash area sampled ($p=0.005$, Fig. 1B). No factors significantly predicted parasitoid abundance or richness (Table S8). Spider abundance tended to increase with more trees and shrubs and spider richness tended to increase with squash area sampled, but no factors significantly predicted spider abundance or richness (Table S8). There was higher ant abundance ($p=0.020$, Fig. 1C) in larger gardens, but no factors predicted ant species richness. Likewise, ladybeetle abundance was higher in larger gardens ($p=0.025$, Fig. 1D), in gardens with more trees and shrubs ($p=0.031$, Fig. 1E). Ladybeetle richness tended to increase with garden size and squash area sampled, and tended to be lower in gardens with higher herbaceous species richness, but no factors significantly predicted ladybeetle richness (Table S8). Predatory Hemiptera abundance was higher in gardens with more squash area ($p=0.016$, Fig. 1F), and with more urban cover ($p<0.001$, Fig. 1G), and tended to increase with number of trees and shrubs in a garden, and predatory Hemiptera richness was higher in gardens with more bare ground ($p=0.007$, Fig. 1H) and higher urban cover ($p=0.007$, Fig. 1I).

Neither herbivore nor natural enemy species composition was significantly influenced by any of the local or landscape factors measured in gardens (Fig. S1, Table S9).

Discussion

This study suggests that factors related to local garden management (e.g., garden size, bare ground, and the number of trees and shrubs) as well as surrounding urban cover in the landscape can strongly influence the abundance and estimated species richness of specific groups of natural enemies, but these same factors do not have significant impacts on herbivores overall or individual herbivore taxa or on composition of natural enemies or herbivores. Moreover, we found that the amount of squash area sampled in a garden impacted several groups of arthropods encountered. But no one variable is indicative of changes to all herbivore or all natural enemy groups. Our results corroborate the findings of Egerer et al. (2017a); Philpott et al. (2014), who found that individual arthropod groups respond to unique environmental variables in urban gardens, thus potentially masking bigger impacts of individual factors on herbivores or natural enemies overall. In the following sections, we discuss possible relationships between specific variables that were significantly and marginally significantly predictive of

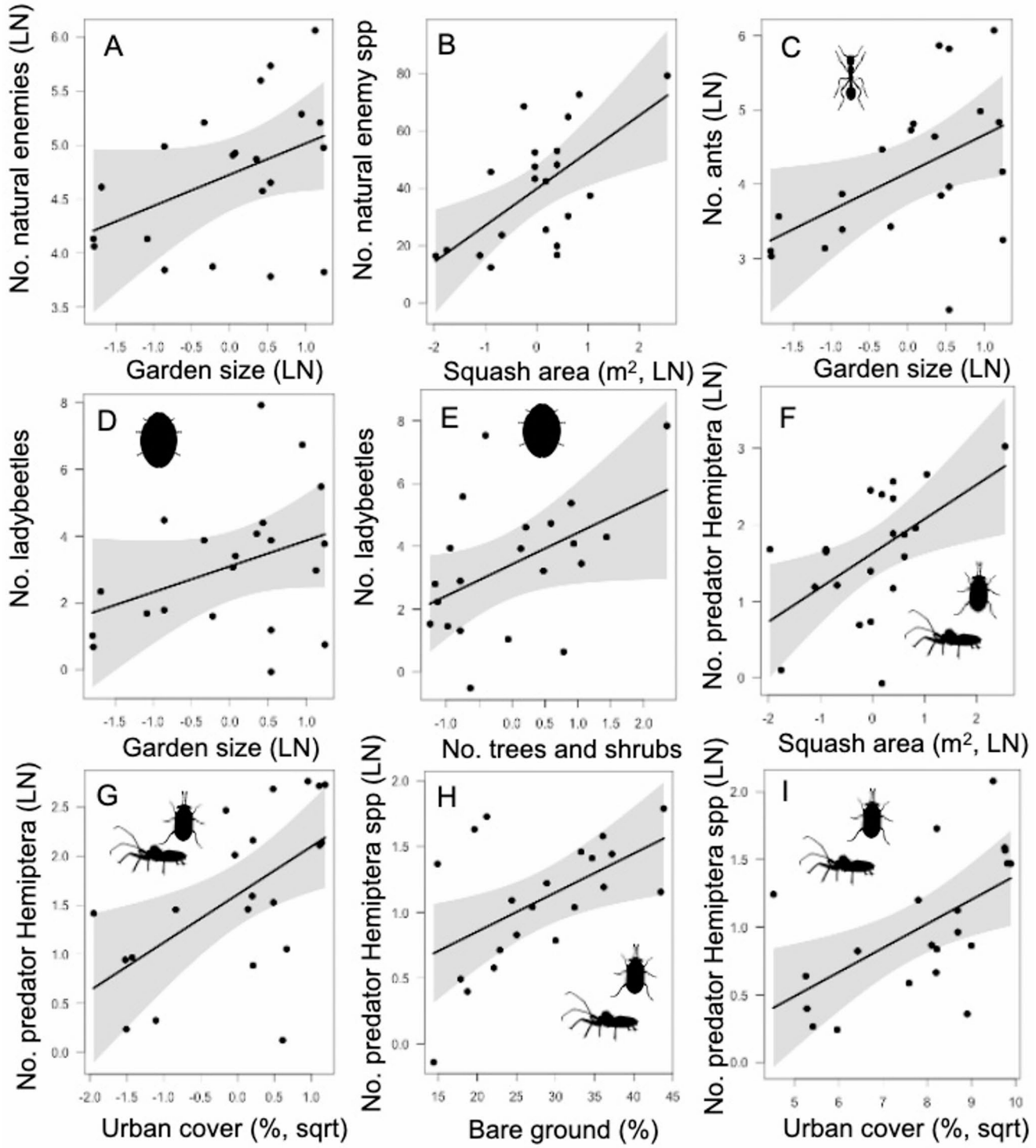

Fig. 1 Local and landscape drivers of natural enemy abudance and estimated species richness in urban agroecosystems in the Centeral Coast of California. Results show significant ($P<0.05$) relationships between natural enemy abundance (**A**), natural enemy estimated species richness (Chao1, **B**), ant abundance (**C**), ladybeetle abundance (**D**, **E**), predatory Hemiptera abundance (**F**, **G**), predatory Hemiptera estimated species richness (Chao1) (**H**, **I**) and garden management and landscape factors. Squash area represents the area of squash sampled in sampled in each garden

Table 1 Summary table of all significant ($P<0.05$) and marginally significant ($0.05<P<0.099$) local and landscape drivers of herbivore and natural enemy abundance and species richness in urban agroecosystems in the California central Coast. Marginally significant effects are shown with parentheses

Group	Arthropod Variable	Squash area	Bare Ground	Herb Spp	No Trees/ Shrubs	Garden Size	Urban Cover
Herbivores	Herbivore abundance			(–)			
	Aphid abundance			(–)			
	Chrysomelidae abundance	(+)		(–)			
	Herbivore Hemiptera	(+)					
Natural Enemies	Natural enemy abundance	(+)				+	
	Natural enemy species richness	+					
	Spider abundance				(+)		
	Spider species richness	(+)					
	Ant abundance					+	
	Ladybeetle abundance			(–)	+	+	
	Ladybeetle species richness	(+)		(–)		(+)	
	Predator Hemiptera abundance	+			(+)		+
	Predator Hemiptera species richness		+				+

herbivore and natural enemy groups. We choose to discuss both significant and marginally significant results as the factors implicated are the same, as are the direction of effects on arthropods. We argue this allows a broader biological assessment of the impacts of garden management on arthropod communities.

We found that an increase in squash area sampled was associated with marginally higher abundance of two herbivores (leaf beetles and herbivore Hemiptera), significantly higher natural enemy species richness and predator Hemiptera abundance, and marginally higher natural enemy abundance, spider species richness, and ladybeetle species richness. These results partially support our prediction that herbivore abundance would be higher in sites with more squash area. We expected that *C. pepo* area sampled might positively influence herbivore abundance following Root's (1973) resource concentration hypothesis, which states that a single-crop structure should be selected by herbivores that prefer a single-host crop. In our sampling effort, we identified four species of abundant Chrysomelidae including *Diabrotica undecimpunctata* (spotted cucumber beetle, $n=32$), *Epitrix* sp. 1 (flea beetle, $n=32$), *Acalymna trivittatum* (striped cucumber beetle, $n=23$), and *Systena* sp. 1 (flea beetle, $n=14$). Both *D. undecimpunctata* and *A. trivittatum* are well-known cucurbit pests that express plant-host preferences due to attraction to cucurbitacin content (Haber et al. 2021). The other two genera of Chrysomelids found also include cucurbit specialist species, thus, finding marginal increases in the abundance of this beetle family with increased squash area was expected. We also found higher abundance or richness of several natural enemies with higher squash area, and this could be due to several reasons. First, this breadth of herbivorous visitors for *C. pepo* may have, in turn, attracted higher abundance and richness of some natural enemy groups. The most abundant predatory Hemiptera observed were multiple species of Anthocoridae ($n=72$), *Nesidiocoris tenuis* (tomato bug, $n=39$), *Geocoris puncticeps* (bigeyed bug, $n=14$), and *Nabis americoferus* (common damsel bug, $n=6$). Anthocorids and *N. americoferus* may both prey on chrysomelid eggs, and thus may have been attracted to sites with higher abundance of chrysomelid prey. Anthocorids also feed on thrips that may be common in *C. pepo* flowers (Letourneau et al. 1990), potentially bolstering abundance of this family. Second, the squash may have provided a structural area promoting predator abundance or richness. Species like *G. puncticeps* may utilize plant structure as undisturbed sites for prey capture or hunting substrate for protection (Decker and Yeargan 2014). Likewise, spider species richness might be expected to increase with *C. pepo* area as some spiders prefer hunting or building webs in plant leaves that offer concealed locations (Nyffeler et al. 1994; Scheidler 1990). Third, omnivory is a life-history strategy known among predatory Hemiptera, like anthocorids, and these predatory Hemiptera species may supplement their diets with plant flowers (such as cucurbits) in the absence of prey (Salas-Aguilar and Ehler 1977; Coll 1998). Fourth, although in each site, we sampled 10 *C. pepo* plants during each of two sampling periods, the size of those plants differed and thus the total area of squash sampled in each garden was different. These increases in both leaf beetle and predator abundance or richness with higher squash area could be merely a sampling effect, meaning that we found more individuals and species because of a larger aboveground biomass sampled.

Among local management features, we found that herbaceous plant species richness had marginally significant effects on several herbivores and one natural enemy taxon, and garden size, bare ground, and the number of trees and shrubs influenced natural enemies. Herbaceous plant species richness was associated with marginally lower abundance

of herbivores, aphids, and leaf beetles, as well as marginally lower abundance and richness of ladybeetles. Declines in herbivores, aphids, and leaf beetles could also be explained by the aforementioned resource concentration hypothesis, whereby having a higher richness of other plants may have confused more specialized herbivores. Concomitant shifts in ladybeetle abundance and richness closely follow, as aphids are a main diet source for ladybeetles and can strongly influence their population sizes and species richness (e.g., Elliott et al. 2002; Parker et al. 2020). Garden size boosted abundance of natural enemies, ants, and ladybeetles, as well as marginal increases in ladybeetle richness. Increased garden area can add places for refuge, habitat, and increased foraging areas in contexts with impervious surface area (Lowenstein and Minor 2018), thereby supporting a higher number of natural enemy species, generally, as well as for ants and ladybeetles. The pattern observed for natural enemies overall was likely driven by an increase in abundance of ants, the most abundant predator encountered. For ants, in particular, larger gardens may support different microclimates or different ways for ants to partition resources. In this study, we encountered five ant species in relatively high abundances: *Linepithema humile* ($n=1467$), *Monomorium ergatogyna* ($n=507$), *Tapinoma sessile* ($n=203$), and *Cardiocondyla mauritanica* ($n=194$). While *L. humile* is an invasive ant and may have negative impacts on overall arthropod diversity in urban areas (Perfecto and Philpott 2023), this ant also provides important biological control in urban agroecosystems (Philpott et al. 2024). Bare ground cover was the one ground cover features included in our final models and we found that this factor boosted the species richness of predatory Hemiptera. This was somewhat unexpected as many studies have documented the importance of different types of ground covers, such as vegetation or mulch, for supporting predatory arthropods (e.g., Sáenz-Romo et al. 2019; Sanchez et al. 2025; Wan et al. 2018). It is possible that interactions between other predators and predatory Hemiptera may have promoted higher Hemiptera richness in gardens with more bare ground. Other studies do find that some predators, such as carabid ground beetles and spiders tend to increase in areas with mulch cover (Otoshi et al. 2015; Egerer et al. 2017b; Philpott et al. 2024), which is strongly negatively correlated with bare ground cover in our study sites. Moreover, Snyder et al. (2022) found that intra-guild predation on Hemiptera was more pronounced in areas with higher prey abundance and richness (such as mulched areas of gardens). This interaction may thus promote predatory Hemiptera in gardens with more bare ground. Finally, we found that a higher number of trees and shrubs was associated with higher abundance of ladybeetles, and marginally higher abundance of spiders and predatory Hemiptera. Shrubs and trees may have offered alternative prey resources (e.g., aphids, scale insects) for ladybeetles. Moreover, shrubs may offer natural enemies, such as *Orius* spp. or other predatory Hemiptera, alternative plant resources like pollen, or oviposition locations (Wilson and Frank 2022, 2023). Addition of trees in gardens may shift the temperature or microclimates of gardens (Brunbjerg et al. 2018) with impacts on development and behavior, thereby influencing the abundance of ladybeetles, spiders, or predator Hemiptera. Thus, gardener decisions to add non-crop diversity like trees and shrubs can serve as a resource addition for predatory species.

At the landscape scale, we observed that urban cover was associated with higher abundance and richness of predatory Hemiptera. Urbanization, or the percent of impervious surface cover and buildings, has been identified as disruptive to biodiversity processes and the ecologies of 'matrix intolerant' insects (Bennett and Gratton 2012; McIntyre 2000). Generalist predators can disperse various kilometers across landscapes (Bianchi et al. 2006; Gardiner et al. 2009), and thus, vegetation patches in the surrounding landscape may provide critical habitat, especially in higher urban cover areas (Bang and Faeth 2011). Although it may seem counterintuitive, urban cover (and lower natural habitat or landscape diversity) sometimes corresponds to increases in diversity and abundance of insects in urban landscapes (e.g.Egerer et al. 2018b; Philpott and Bichier 2017). This may be because floral abundance and richness is much higher in irrigated urban areas like gardens during the summer months (June-August) compared with semi-natural habitats in the areas surrounding urban areas (Philpott et al. 2025), thereby boosting floral and prey resources for predatory Hemiptera during this time of year. Alternatively, urban gardens may provide habitat refuges for arthropods in urban areas leading to landscape-level resource concentration, or more suitable temperatures compared to surrounding habitats (e.g., Fenoglio et al. 2009). Thus, identifying how green spaces such as lawns, home gardens, native vegetation, and landscaping that surround urban garden sites may be able to provide better resources is highly important (Burkman and Gardiner 2014).

Conclusion

Our study identified that no single local or landscape factor predicts the abundance or species richness of all herbivores or predators, or even of all herbivore or predator groups. Instead, we document several local management factors (garden size, ground cover, herbaceous plant species richness, and number of trees and shrubs) play a role in shaping unique groups of herbivores and natural enemies. While select local factors did not predict shifts in abundance or richness of all natural enemy or herbivores groups

examined, effects were consistent for those groups responding to local management shifts. Moreover, landscape surroundings (urban cover) shape the abundance of some natural enemies found on *C. pepo* in urban gardens. Understanding the impacts of local and landscape management in and around urban gardens on natural enemies is essential because they contribute to herbivore regulation (Gardiner et al. 2009; Snyder et al. 2006). However, changes in natural enemy diversity and composition may only sometimes lead to pest suppression, potentially due to context-specific habitat factors, indirect effects, or limitations to measurement efforts (Karp et al. 2018; Letourneau et al. 2011). Thus, enhancing conservation efforts for natural enemies and increasing the potential of conservation biological control through habitat management represents a challenge in urban gardens. Although landscape-level changes strongly impact insects and spiders, landscape management is usually outside of urban community gardener control. Thus, community garden or plot-level adaptations remain essential to study because these options are accessible to gardeners (Tooker et al. 2020).

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Author contributions EMG conducted fieldwork, lab work, data analysis, and focal crop selection, and wrote the first draft of the manuscript. MMS participated in insect identification. SMP designed the field research, and contributed to logistics, data analysis, manuscript writing, and editing.

Data availability Data will be made available on AgCommons once the manuscript is accepted for publication.

Declarations

Competing interests The authors declare no competing interests.

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