

UC Santa Cruz

UC Santa Cruz Previously Published Works

Title

Natural enemy–herbivore networks along local management and landscape gradients in urban agroecosystems

Permalink

<https://escholarship.org/uc/item/8vb4h0qc>

Journal

Ecological Applications, 30(8)

ISSN

1051-0761

Authors

Philpott, Stacy M
Lucatero, Azucena
Bichier, Peter
[et al.](#)

Publication Date

2020-12-01







DOI

10.1002/eap.2201

Peer reviewed



Natural enemy–herbivore networks along local management and landscape gradients in urban agroecosystems

STACY M. PHILPOTT ^{1,5}, AZUCENA LUCATERO ¹, PETER BICHIER,¹ MONIKA H. EGERER ^{1,6}, SHALENE JHA ²,
BRENDA LIN ³, AND HEIDI LIERE ⁴

¹Environmental Studies Department, University of California, Santa Cruz, 1156 High Street, Santa Cruz, California 95064 USA

²Department of Integrative Biology, University of Texas at Austin, 205 W. 24th Street, 401 Biological Laboratories, Austin, Texas 78712 USA

³CSIRO Land and Water Flagship, EcoSciences Precinct, 41 Boggo Road, Dutton Park, Queensland 4102 Australia

⁴Department of Environmental Studies, Seattle University, 901 12th Avenue, Casey 210, Washington 98122 USA

Citation: Philpott, S. M., A. Lucatero, P. Bichier, M. H. Egerer, S. Jha, B. Lin, and H. Liere. 2020. Natural enemy–herbivore networks along local management and landscape gradients in urban agroecosystems. *Ecological Applications* 00(00):e02201. 10.1002/eap.2201

Abstract. Ecological networks can provide insight into how biodiversity loss and changes in species interactions impact the delivery of ecosystem services. In agroecosystems that vary in management practices, quantifying changes in ecological network structure across gradients of local and landscape composition can inform both the ecology and function of productive agroecosystems. In this study, we examined natural-enemy–herbivore co-occurrence networks associated with *Brassica oleracea* (cole crops), a common crop in urban agricultural systems. Specifically, we investigated how local management characteristics of urban community gardens and the landscape composition around them affect (1) the abundance of *B. oleracea* herbivores and their natural enemies, (2) the natural-enemy: herbivore ratio, and (3) natural-enemy–herbivore co-occurrence network metrics. We sampled herbivores and natural enemies in *B. oleracea* plants in 24 vegetable gardens in the California, USA central coast region. We also collected information on garden characteristics and land-use cover of the surrounding landscape (2 km radius). We found that increased floral richness and *B. oleracea* abundance were associated with increased parasitoid abundance, non-aphid herbivore abundance, and increased network vulnerability; increased vegetation complexity suppressed parasitoid abundance, but still boosted network vulnerability. High agricultural land-use cover in the landscape surrounding urban gardens was associated with lower predator, parasitoid, and non-aphid herbivore abundance, lower natural-enemy: herbivore ratios, lower interaction richness, and higher trophic complementarity. While we did not directly measure pest control, higher interaction richness, higher vulnerability, and lower trophic complementarity are associated with higher pest control services in other agroecosystems. Thus, if gardens function similarly to other agroecosystems, our results indicate that increasing vegetation complexity, including trees, shrubs, and plant richness, especially within gardens located in intensively farmed landscapes, could potentially enhance the biodiversity and abundance of natural enemies, supporting ecological networks associated with higher pest control services.

Key words: *Brassica oleracea*; California central coast; ecological network; food web; interaction richness; parasitoid; predator; trophic complementarity; urban community garden.

INTRODUCTION

Urban agroecosystems, or urban farms and gardens, provide an ideal model agricultural system in which to examine how changes in agricultural and landscape management practices affect species richness, species

interactions, and ecosystem services (Egerer et al. 2017a, Philpott and Bichier 2017). Urban gardens are productive and diverse agroecosystems (Lin et al. 2015) that provide a substantial part of the global food supply (Smit et al. 1996, Hodgson et al. 2011) and promote gardener health and well-being (Brown and Jameton 2000, Classens 2015). Urban gardeners often refer to nutritional and cultural services as primary reasons for urban cultivation, yet they also cite challenges with management as they lack information on how to optimize ecosystem services such as pest control, pollination, and crop production (Oberholtzer et al. 2014). In other words, while urban agroecosystems have the potential to

Manuscript received 23 November 2019; revised 15 April 2020; accepted 6 May 2020. Corresponding Editor: Alison K. Brody.

⁵Present address: Department of Ecology Ecosystem Science, Plant Ecology Technische Universität Berlin Rothenburgstrasse 12 12165 Berlin Germany

⁶E-mail: sphilpot@ucsc.edu

address a range of societal needs, we currently lack a mechanistic understanding of how garden and landscape management practices impact biodiversity and key ecosystem services, such as pest control. Providing this ecological understanding is vital given the increased importance of urban agriculture for food security, especially in underserved communities with limited food access (Alig et al. 2004, Pothukuchi and Thomas 2004, Ver Ploeg et al. 2009, Chappell and LaValle 2011).

Urban agroecosystems often fall along gradients of local management and landscape intensification that can strongly impact the abundance, richness, and composition of natural enemies, their herbivore prey, and pest control services provided. Local-scale vegetation diversity and complexity as well as higher floral abundance and richness boost abundance and richness of natural enemies (Andow 1991, Langelotto and Denno 2004). Landscapes with higher amounts of natural habitat cover offer more resources for beneficial insects (Landis et al. 2000) and support a higher density and diversity of arthropods, even when local sites have low vegetation diversity (Bianchi et al. 2006). In urban agroecosystems, in particular, pest control providers, or natural enemies (such as spiders, carabids, ladybeetles, and parasitoids), respond to unique, garden-specific local (e.g., soil quality, ground cover, vegetation diversity) and landscape characteristics (e.g., natural habitat cover; Colding et al. 2006, Bennett and Gratton 2012, Burkman and Gardiner 2014, Otoshi et al. 2015, Burks and Philpott 2016, Delgado de la Flor et al. 2017, Egerer et al. 2017*b*). Moreover, the level of pest suppression may depend on within-garden management (Philpott and Bichier 2017, but see Gardiner et al. 2014), but not enough is known about the mechanisms underlying this suppression and whether or not shifts in biodiversity of key natural enemy species influence natural enemy–herbivore networks in urban agroecosystems. While increasing biodiversity (e.g., of natural enemies) is often associated with increases in ecosystem services (Tscharrntke et al. 2012), this is not always the case (Cardinale et al. 2006). One potential explanation is that ecosystem services depend on the structure of ecological networks (Lavelle and Garnier 2002, Schleuning et al. 2015, Perović et al. 2018), not biodiversity alone.

Ecological network analysis is a powerful tool for understanding food-web and community dynamics (Bascompte et al. 2003) and can increase our understanding of how changes in local and landscape management affect diversity, with possible subsequent impacts on ecosystem services (Perrings et al. 2010, Bohan et al. 2013, Woodward and Bohan 2013, Tylianakis and Binzer 2014). Networks depict ecological interactions between species across adjacent trophic levels (Bascompte et al. 2003, Ings et al. 2009) where species are often referred to as nodes and pairwise interactions between species are referred to as links. Metrics that quantify network structure can reveal a number of ecologically relevant features, such as ecological redundancy

and robustness of a community, dependence of one trophic level on another, and the number of distinct functional groups within a network (Bascompte et al. 2003, Blüthgen et al. 2007, Devoto et al. 2012). Analysis of networks is thus an important tool for understanding how community characteristics relate to ecosystem function and services (Perrings et al. 2010, Bohan et al. 2013, Woodward and Bohan 2013, Tylianakis and Binzer 2014). Network configuration and patterns of interactions could also yield insight into relationships between biodiversity, stability, and resilience (Bohan et al. 2013, Woodward and Bohan 2013), and network metrics are often utilized to predict ecosystem service responses to perturbations (Bluthgen 2010). However, it is still unclear how networks change along agricultural management gradients, or how these changes impact ecosystem function and services (Thompson et al. 2012). While some studies have found no structural changes in trophic (or antagonistic) networks and associated parasitism rates along agricultural management gradients (Gagic et al. 2012), others have found that low habitat complexity can improve predator search efficiency, effectively increasing the number of species interactions (Laliberté and Tylianakis 2010) or increasing attack rates on preferred resources, thereby lowering interaction evenness (Tylianakis et al. 2007, Rodewald et al. 2015).

To our knowledge, no studies have specifically examined antagonistic trophic networks along an urban garden management or urban landscape gradient. To work toward filling this gap in the literature, we quantified the abundance and composition of natural enemies and herbivores, as well as natural-enemy–herbivore co-occurrence networks, within urban agroecosystems that vary in both local management characteristics (e.g., vegetation and ground cover characteristics) and landscape surroundings (e.g., percent of the surrounding landscape in urban impervious cover, natural habitat, and agriculture). Specifically, we asked (1) how do natural enemy and herbivore abundance, and natural-enemy:herbivore ratios differ in response to local management and landscape characteristics of urban gardens, (2) how do natural-enemy–herbivore network metrics differ in response to local management and landscape characteristics of urban gardens, and (3) what are the implications for pest suppression in urban gardens, given these differences in network metrics?

METHODS

Study system

We studied natural enemy (predator and parasitoid) and herbivore abundance and co-occurrence networks in urban gardens in the California central coast region between May and August 2017. We selected 24 urban community gardens in Monterey (seven gardens), Santa Cruz (nine gardens), and Santa Clara (eight gardens) counties for field research (Fig. 1). The sites within these

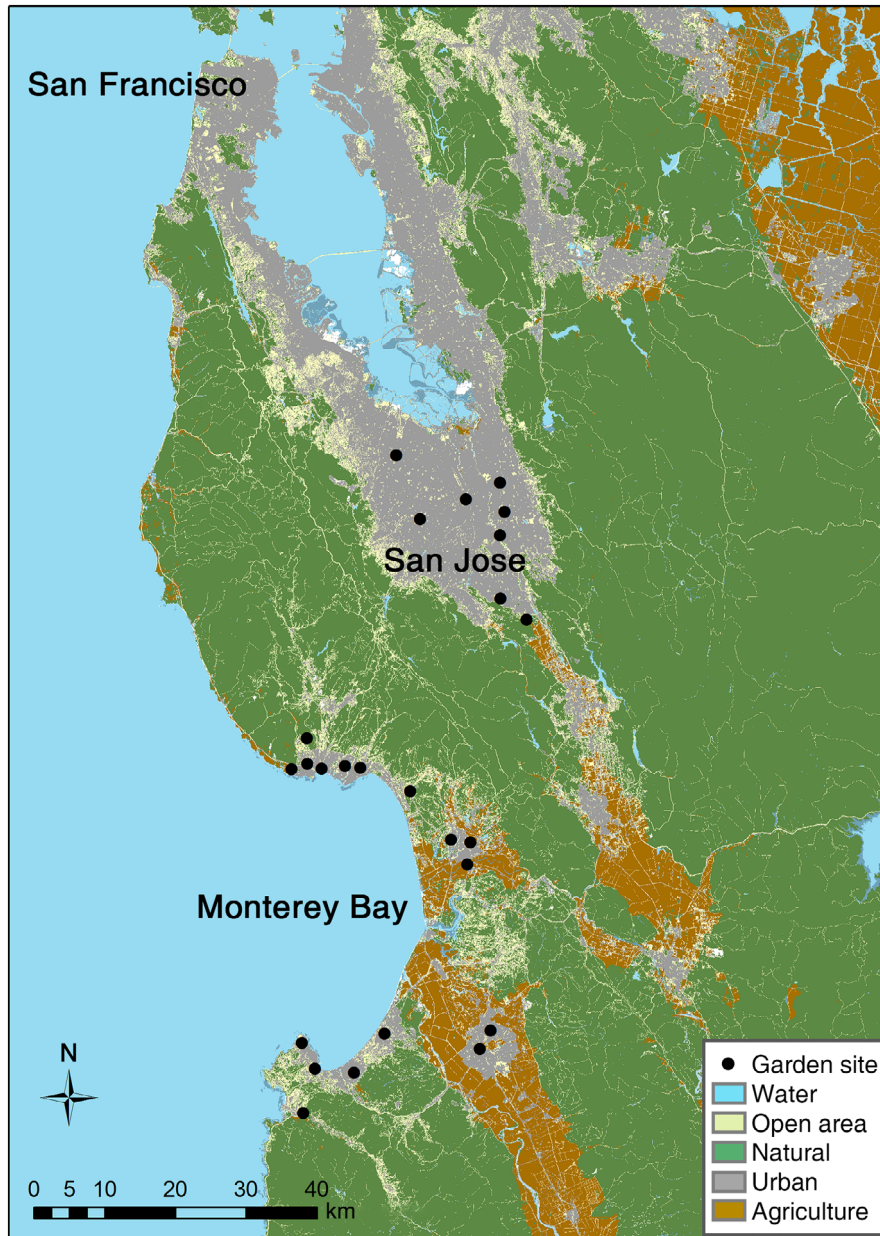


FIG. 1. Map of the urban community garden study sites and landscape surroundings. The four land use types (open, urban, natural, and agriculture) were created using National Landcover Database cover classes and are fully described in *Methods*.

three counties are distributed in two different California ecoregions, the Monterey Bay Plains and Terraces (Santa Cruz and Monterey County sites) and the Bay Terraces/Lower Santa Clara Valley (Santa Clara County sites), which are broadly different in terms of biotic and abiotic phenomena that may influence the ecology of those systems (Griffith et al. 2016). All gardens are community gardens (with vegetables, fruit trees, and ornamental plants) managed collectively or in individual allotments (plots), and the gardens range in size from

444 m² to 15,400 m². Each garden had been in production for between 2 and 50 yr during the time of the study. All gardens were separated from each other by a minimum of 2 km (Fig. 1). Several studies from this system have documented various local and landscape drivers of herbivore and natural enemy abundance and richness (Otoshi et al. 2015, Egerer et al. 2017a), natural enemy traits (Liere et al. 2019, Philpott et al. 2019), dispersal (Egerer et al. 2018a), and pest control services (Philpott and Bichier 2017).

Natural enemy and herbivore surveys and identification

We surveyed gardens four times over the summer growing season for natural enemies and herbivores (15–19 May, 19–23 June, 17–20 July, and 14–17 August 2017). We chose to survey arthropods on *Brassica oleraceae* as a model system as this is one of the few crops present and abundant in all sites and because this is a common crop in large farms within the study region (Egerer et al. 2018b). We haphazardly selected up to 20 *B. oleraceae* plants within a 20 × 20 m plot located in the center of each garden. If there was more than one variety of *B. oleraceae* in the plot (e.g., broccoli, curly kale, cabbage), or more than 20 individual plants, we selected plants to represent the relative abundance of different varieties and spatial distribution across the plot. We measured the height and width, the flowering status, and the variety (e.g., curly kale, broccoli) of all surveyed plants. We visually examined all above ground plant parts (e.g., leaves, stems, fruits, flowers) of each plant for arthropods. We then manually collected all arthropods encountered either directly on the plant or hovering above the plant using forceps and vials. The exception was cabbage aphids (*Brevicoryne brassicae*), which we counted but did not collect due to their high densities and easy identification. All collected arthropods were placed into a vial with 70% ethanol and individually marked.

We identified all arthropods to order, family, genus, or species as necessary to determine the trophic guild of the arthropod (e.g., herbivore, parasitoid, predator). We identified the trophic guilds following Borror and White 1970, Marshall 2006, and online identification resources (AphID 2017, BugGuide 2017, UC IPM 2017). In cases where we failed to collect an arthropod (e.g., it flew away before collection), we described the arthropod and noted the order or family as possible. Only those arthropods that were collected or described at least to order were included in the analyses. See Appendix S1: Table S1 for a list of all natural enemies collected and Appendix S1: Table S2 for a list of all herbivores collected.

Vegetation, ground cover, and landscape characteristics

Within the 20 × 20 m plot at the center of each garden, we sampled vegetation and ground cover characteristics. We sampled canopy cover with a concave spherical densiometer at the center of each plot, and 10 m to the north, south, east, and west of the center. We counted the number of trees and shrubs, the number of tree and shrub species, the number of trees and shrubs in flower, and the number of tree and shrub species in flower. We also counted the total number of *B. oleraceae* plants within the 20 × 20 m plot, and the number of *B. oleraceae* plants sampled during each visit. Within the 20 × 20 m plots, we randomly selected eight 1 × 1 m plots within which we identified all herbaceous plants (except grass) to morphospecies; counted the number of

flowers and number of species in flower; measured the height of the tallest herbaceous vegetation; and visually estimated the percent of the plot covered by (1) bare ground, (2) grass, (3) herbaceous plants, (4) rocks, (5) leaf litter, (6) straw, and (7) mulch or wood chips. We took vegetation and ground cover data on the same days that we sampled arthropods, and all values for each site (except for herbaceous species richness) were averaged across the four sample dates. For herbaceous species richness, we estimated the total herbaceous plant species richness (Chao1) in each site across all sample dates with the estimateR function in the vegan package for R (Oksanen et al. 2018, R Development Core Team 2018). We calculated a vegetation complexity index (VCI) for each site (Philpott et al. 2008). To calculate the VCI, we included canopy cover, number of trees and shrubs, number of tree and shrub species, the number of trees and shrubs in flower, the number of trees and shrubs and tree and shrub species in flower, estimated species richness of herbaceous plant species, herbaceous plant cover, and height of the tallest vegetation. We scaled values for each variable from 0 to 1 by dividing by the highest value measured across all sites. We then averaged values for the eight variables to yield an overall VCI between 0 (low vegetation complexity) and 1 (high vegetation complexity). Thus, overall, we collected or calculated a total of 18 vegetation and ground cover variables in each garden (Appendix S1: Table S3).

We used land-cover data from the 2011 National Land Cover Database (NLCD, 30-m resolution; Homer et al. 2015) and calculated the percentage of land-cover types in 2-km buffers from the center of each garden. We created four land-cover categories: (1) natural (including the NLCD categories of deciduous, evergreen, and mixed forests, dwarf scrub, shrub/scrub, and grassland/herbaceous), (2) open (including lawn grass, 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 types covered <5% of the surrounding landscape and were not included. We used the vegan package in R (Oksanen et al. 2018, R Development Core Team 2018) to calculate landscape diversity (e.g., modified Shannon-Wiener diversity index, H') for each garden at the 2-km scale, as in McGarigal et al. 2002 (also see Bennett and Gratton 2012). Thus, we calculated a total of five landscape variables for the analysis (Table S3).

Natural-enemy–herbivore network construction

We constructed natural enemy networks based on positive co-occurrence of families of natural enemies (predators or parasitoids) and herbivores on the same plant (as in Bell et al. 2010). For each site, we calculated the mean number of aphids, non-aphid herbivores, predators, parasitoids, and natural enemies (predators plus parasitoids) per *B. oleraceae* plant. In order to estimate feeding links between individual families of natural

enemies and herbivores, we used qualitative diet and host information for all the observed predator and parasitoid taxa from the literature. We searched general entomology books (see Appendix S1: Table S4) and specialized pest control websites (UC IPM 2017) to determine reported predator-prey and parasitoid-host connections for each observed family. If we could not find reports of interactions between two families, and determined it unlikely that an interaction was not possible due to mouth-part or physiological constraints, we marked this as a “forbidden” link and used a different notation in our data set to build the network and to differentiate from true zeroes (Jordano 2016; Appendix S1: Table S5).

We examined three network metrics: estimated interaction richness, vulnerability, and trophic complementarity. We chose these three metrics because there is empirical or theoretical evidence that pest control functions should change as these metrics change (Bersier et al. 2002, Tylianakis et al. 2010, Gagic et al. 2012, Fabian et al. 2013, Poisot et al. 2013). Specifically, interaction richness measures the ecological redundancy and robustness of a community (Bascompte et al. 2003, Blüthgen et al. 2007, Devoto et al. 2012). Vulnerability is a measure of the average number of natural enemy species per prey species (Bersier et al. 2002, Tylianakis et al. 2007, Blüthgen 2010). Trophic complementarity represents the degree to which natural enemies share prey resources, and is often used as a predictor of pest control (Poisot et al. 2013, Peralta et al. 2014). To calculate estimated interaction richness, we first noted each positive co-occurrence of natural-enemy–herbivore family pairs in each site, tallied abundance as the number of plants on which that family pair co-occurred, and then used the estimateR function with the vegan package in R (Oksanen et al. 2018, R Development Core Team 2018) to calculate Chao1 (abundance-based) estimated interaction richness for each site, as in Jordano 2016. Use of estimated interaction richness, rather than simple numbers of interactions, buffers against lower sample sizes in network studies (Jordano 2016). We used the bipartite package in R (Dormann et al. 2008) to calculate vulnerability, a measure of the mean number of natural enemy families per herbivore family (Tylianakis et al. 2007), and NDOF (nestedness metric based on overlap and decreasing fill; Almeida-Neto et al. 2008). We then calculated trophic complementarity (C , a measure of the shared natural enemy families for each herbivore) following Poisot et al. 2013 who model this as the inverse of NDOF where $C = (100 \times \text{NDOF})/100$. For calculating network metrics, we used site as the replicate and the number of plants within a site on which a natural enemy and herbivore family co-occurred as our metric of abundance.

Data analysis

Because of the large number of predictor variables collected, and the potential for collinear variables, we first

ran Pearson’s correlations to identify correlated variables and to select variables for subsequent analysis (Table S3). We grouped variables into biologically relevant groups (e.g., vegetation variables, ground cover variables, landscape variables). We then identified variables that were significantly correlated with one another and selected one variable per group to include in further analysis. Of the correlated variables, we selected the one with the highest average correlation coefficients with other variables. We also selected variables that were not correlated with any others. Based on the Pearson’s correlations, we selected a total of nine explanatory variables: VCI, number of *B. oleraceae* per plot, ecoregion, garden size, percent bare ground, percent grass, number of flower species, agriculture within 2 km, and urban land cover within 2 km (Table S3). We used natural-log-transformed (garden size, number of *B. oleraceae* plants) or square-root-transformed (grass cover in 1×1 m plots, agriculture cover within 2 km, and urban land cover within 2 km) data for some variables to improve model fit. Because correlation coefficients only consider pairwise comparisons, and to assure that we did not have collinearity between some of the remaining explanatory variables (Zuur et al. 2009), we checked the variable inflation factor (VIF) with the vif function in the car package version 3.0-2 (Fox and Weisberg 2011). Initial tests indicated that urban cover within 2 km was collinear with other variables: after removing that variable from our global model, all VIF scores were below 2.3.

To examine which local and landscape factors drive changes in natural enemy and herbivore abundance, natural-enemy:herbivore ratio, and network metrics, we used generalized linear models (GLMs) with the glm function in R (R Development Core Team 2018). For herbivore and natural enemy variables, we examined aphid abundance, non-aphid herbivore abundance, predator abundance, parasitoid abundance, and the ratio of natural enemies to herbivores as dependent variables in our models. To examine changes in network metrics, we used estimated interaction richness, vulnerability, and trophic complementarity as dependent variables. For each of the dependent variables, we tested all combinations of the eight selected explanatory variables with the glmulti function (Calcagno and de Mazancourt 2010) and selected the top model based on the Akaike information criterion corrected for sample size (AIC_c) values. For all models where the AIC_c value was within two points of the next best model, we averaged models with the model.avg function in the MuMIn package (Barton 2012) and report conditional averages for significant model factors. For all dependent variables (except trophic complementarity), we used a negative binomial distribution as this provided the best fit (e.g., relatively equal residual deviance and df values and nonsignificant asymptotic chi-square tests for goodness of fit). For trophic complementarity, a Gaussian distribution provided the best fit. We visualized all significant local and landscape predictors of prey removal from either top

models or the averaged top model with the visreg package in R (Breheny and Burchett 2013). All statistical analyses were conducted in R version 1.1.456 (R Development Core Team 2018).

Due to the importance of agricultural cover in the landscape in many models (see *Results*), and a relatively small number of sites with agriculture in the landscape ($n = 6$), we performed a subsequent analysis as described above, only including sites with no agriculture in the landscape ($n = 18$) to determine which local and landscape factors drove variation in natural enemy and herbivore abundance and network metrics in those sites. For those models, we included VCI, number of *Brassica* per plot, percent bare ground, percent grass, number of flowering species, and urban land cover within 2 km to maintain VIF scores below 1.65. We did not include ecoregion or garden size in these models due to high collinearity.

RESULTS

We recorded a total of 69,006 arthropods representing 60 families sampled from 216.87 m² of *B. oleracea* vegetation in the gardens. The most common orders we collected were Hemiptera, Lepidoptera, Hymenoptera, Diptera, Araneae, and Coleoptera and the most common families were Aphididae ($n = 1341$), Aleyrodidae ($n = 233$), Syrphidae ($n = 173$), Theridiidae ($n = 102$), Cicadellidae ($n = 87$), Braconidae ($n = 73$), Formicidae ($n = 65$), Coccinellidae ($n = 62$), Chrysomelidae ($n = 60$), Linyphiidae (Erigoninae; $n = 58$), Pentatomidae ($n = 45$), and Figitidae ($n = 38$).

Across all sites, natural enemy abundance, herbivore abundance, and natural-enemy:herbivore ratio responded to two local factors and one landscape factor (Table 1, Fig. 2). Non-aphid herbivore abundance increased with more *Brassica* plants per plot (Fig. 2a) and decreased with increases in agriculture in the landscape (Fig. 2b). The number of parasitoids decreased with increases in VCI (Fig. 2d), increased as floral species richness increased (Fig. 2e), and the abundance of both predators and parasitoids decreased with increasing agriculture in the landscape (Fig. 2f, g). The natural-enemy:herbivore ratio decreased (i.e., fewer natural enemies per herbivore) as the amount of agriculture in the landscape increased (Fig. 2h). No other factors included in any other top statistical models were significant predictors of any dependent variable (Table 1). For sites without agriculture in the landscape, herbivore abundance responded to only one local factor, but no landscape factors (Table 2). The number of non-aphid herbivores increased with the number of *Brassica* plants in the garden (Fig. 2c).

Across all sites, one local and one landscape factor influenced natural-enemy–herbivore network metrics. Estimated interaction richness decreased with increases in agricultural cover in the landscape (Fig. 2i) and trophic complementarity increased as the amount of

TABLE 1. Results of GLM models examining relationships between local and landscape features of urban gardens and natural enemy abundance, herbivore abundance, natural-enemy:herbivore ratio, and natural-enemy–herbivore network metrics across all study sites.

Dependent variable and factors in averaged model	No. models factor was included†	<i>z</i>	<i>P</i>
No. aphids			
Garden size‡	1	1.448	0.148
No. non-aphid herbivores			
Agriculture 2 km§	1	2.012	0.044
No. <i>Brassica</i> per plot‡	1	1.687	0.092
VCI	1	1.365	0.172
No. parasitoids			
Agriculture 2 km§	8	2.454	0.014
No. flower species	5	1.655	0.098
Grass 1 m§	2	1.633	0.102
Bare 1 m	2	0.342	0.179
VCI	1	2.072	0.038
Ecoregion	1	1.103	0.277
No. predators			
Agriculture 2 km§	2	2.634	0.008
Garden size‡	1	1.418	0.156
Natural enemy:herbivore ratio			
Agriculture 2 km§	3	1.668	0.095
Ecoregion	2	1.396	0.162
Garden size‡	2	0.992	0.321
VCI	1	0.959	0.337
Bare 1 m	1	0.878	0.380
Trophic complementarity, <i>C</i>			
Agriculture 2 km§	2	3.053	0.002
No. flower species	1	1.23	0.218
Vulnerability			
No. <i>Brassica</i> per plot‡	6	2.083	0.037
Agriculture 2 km§	9	1.532	0.125
Grass 1 m§	2	1.586	0.113
Garden size‡	6	1.12	0.263
Bare 1 m	2	1.117	0.264
Ecoregion	1	1.392	0.164
Estimated interaction richness (Chao1)			
Agriculture 2 km§	3	3.797	<0.001
No. flower species	2	1.476	0.139
No. <i>Brassica</i> per plot‡	1	1.81	0.070

Note: Grass 1 m, the percent grass cover in 1x1 m plots; Bare 1 m, the percent bare ground cover in 1x1 m plots; Agriculture 2 km, the percent agriculture cover within 2 km of garden sites; VCI, vegetation complexity index.

†Number of top models included in average model for each dependent variable was as follows: no. aphids (2), no. non-aphid herbivores (4), no. parasitoids (8), no. predators (2), natural-enemy:herbivore ratio (8), trophic complementarity (2), vulnerability (15), estimated interaction richness (3).

‡ln-transformed.

§Square-root-transformed.

intensive agriculture in the landscape increased (Fig. 2j). Other factors were included in top statistical models, but no other factors predicted changes in network metrics (Table 1). For sites without agriculture in the landscape,

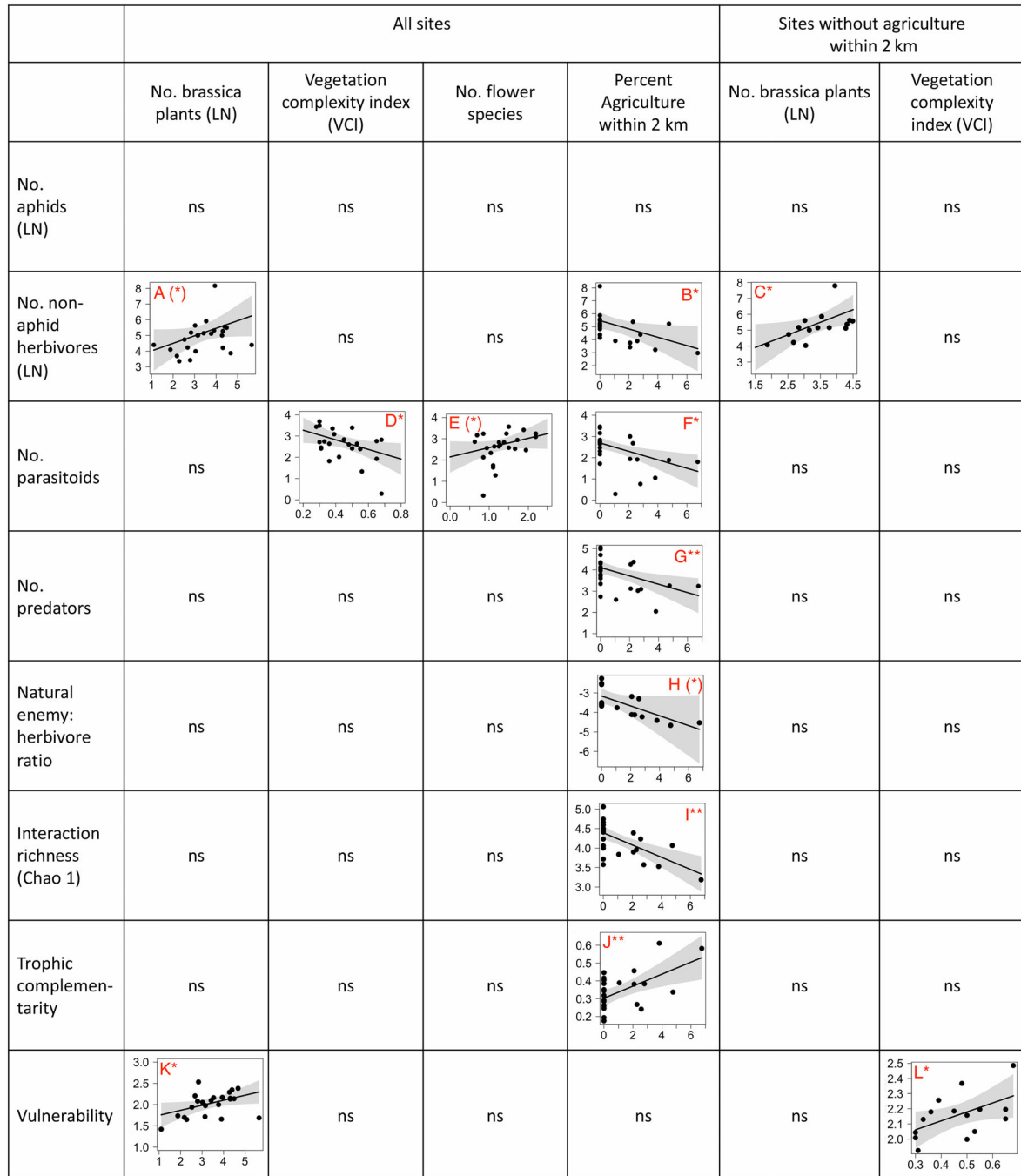


FIG. 2. Results from general linear models (GLM) examining relationships between local (vegetation complexity index [VCI], no. flower species, no. *B. oleracea* plants) and landscape (percent agriculture within 2 km) features of urban community gardens and abundance of herbivores, natural enemies, natural enemy to herbivore ratio, and three network metrics. See Tables 1 and 2 for details on which factors were included in best or averaged GLM models. Points show individual garden study sites and gray bands show 95% confidence bands. Significance is denoted as (*) for *P* values between 0.05–0.10, as * for values between 0.01–0.05, as ** for values <0.01, and as ns for nonsignificant relationships.

network metrics shifted with just one local factor (Table 2). Network vulnerability increased with VCI (Fig. 2I).

Visualization of the natural-enemy–herbivore networks shows clear structural differences in the network structure with varying floral species richness and

TABLE 2. Results of GLM models examining relationships between local and landscape features of urban gardens and natural enemy abundance, herbivore abundance, natural-enemy:herbivore ratio, and natural enemy - herbivore network metrics for sites without agriculture in the landscape.

Dependent variable and factors in averaged model	No. models factor was included†	<i>z</i>	<i>P</i>
No. aphids			
VCI	1	1.278	0.201
Grass 1 m‡	1	1.097	0.273
No. non-aphid herbivores			
No. <i>Brassica</i> per plot§	1	1.985	0.047
Grass 1 m‡	1	1.286	0.196
No. parasitoids			
No. <i>Brassica</i> per plot§	1	1.149	0.251
No. flower species	1	0.960	0.337
No. predators			
VCI	1	1.386	0.166
Grass 1 m‡	1	1.057	0.290
Urban 2 km‡	1	0.886	0.375
Natural enemy: herbivore ratio			
Intercept only	NA	NA	NA
Trophic complementarity, <i>C</i>			
VCI	1	0.513	0.13
No. flower species	1	1.421	0.155
Bare 1 m	1	0.210	0.226
Vulnerability			
VCI	2	1.967	0.049
No. <i>Brassica</i> per plot§	2	1.550	0.121
Estimated interaction richness (Chao1)			
No. flower species	1	1.484	0.138

Note: Urban 2 km is the percent of urban developed land within 2 km of garden sites.

†Number of top models included in average model for each dependent variable was as follows: no. aphids (3), no. non-aphid herbivores (3), no. parasitoids (3), no. predators (4), natural-enemy: herbivore ratio (best), trophic complementarity (4), vulnerability (4), estimated interaction richness (2).

‡Square-root-transformed.

§ln-transformed.

agricultural cover in the 2 km surrounding each garden (Fig. 3).

DISCUSSION

In this study, we found that the abundance of natural enemies and herbivores, their associations, as well as their co-occurrence network structure vary with both local management and landscape characteristics of urban gardens. Specifically, across all sites, we found that both local and landscape factors strongly predict natural enemy and herbivore abundance, ratios, and network metrics; however, in sites without agriculture in the landscape, only local habitat features mattered.

The three local factors that were significant or marginally significant predictors of changes in natural enemy

and herbivore abundance and network metrics in this system were *Brassica* abundance, floral richness, and vegetation complexity; while all three have been associated with increases in natural enemy abundance and richness in rural and urban agroecosystems, their relationship with ecological networks had never been investigated before. To begin, our finding that an increase in *Brassica* abundance was associated with higher non-aphid herbivore abundance is not surprising given that a larger resource base can support a higher abundance of herbivores. Several studies document that aspects of vegetation complexity in gardens can affect natural enemies; for example, high diversity of flowering vegetable, fruit, and ornamental plants (Colding et al. 2006) and taller vegetation (Delgado de la Flor et al. 2017) provide nectar and other resources and support greater abundance and diversity of natural enemies (Burkman and Gardiner 2014). In particular, parasitoids benefit from floral abundance, tall herbaceous vegetation, and trees and shrubs (Raupp et al. 2010, Burks and Philpott 2016, Egerer et al. 2017a); ladybeetles benefit from high ornamental plant abundance and crop richness (Egerer et al. 2017b); and spiders benefit from high plant richness in gardens (Otoshi et al. 2015). In this study, increases in floral species richness tended to boost parasitoid abundance, confirming previous studies. Yet, parasitoid abundance surprisingly decreased with increases in overall vegetation complexity in the gardens, inconsistent with previous studies in gardens. We also documented that increasing *Brassica* abundance boosted network vulnerability, indicating greater enemy diversity and abundance per herbivore. One past study examining network structure differences across agricultural management types found higher vulnerability in structurally simple tropical agroecosystems (Tylianakis et al. 2007), but this study included a much more extreme gradient of agricultural systems (shaded coffee agroforests to monoculture rice) in contrast to our study system, where we controlled for the same local agricultural type. Thus, perhaps larger landscape-level shifts toward simplified monoculture systems may increase vulnerability whereas smaller vegetation changes to a relatively complex urban agroecosystem may enhance vulnerability. Another study examining impacts of vegetation and landscape changes on vulnerability in parasitoid–host networks failed to find any impact of the vegetation richness or biomass, but found strong impacts of landscape-level forest cover on vulnerability, interaction diversity, generality, and link density (Fabian et al. 2013). Interestingly, in our study, *Brassica* abundance and vegetation complexity were important predictors of herbivores, natural enemies, and network metrics across all sites and also for those sites without any agriculture in the landscape.

We found that increasing agricultural cover in the landscape was indicative of lower abundance of predators, parasitoids, and non-aphid herbivores; a lower natural-enemy:herbivore ratio; lower interaction richness; and higher trophic complementarity. Further, in sites

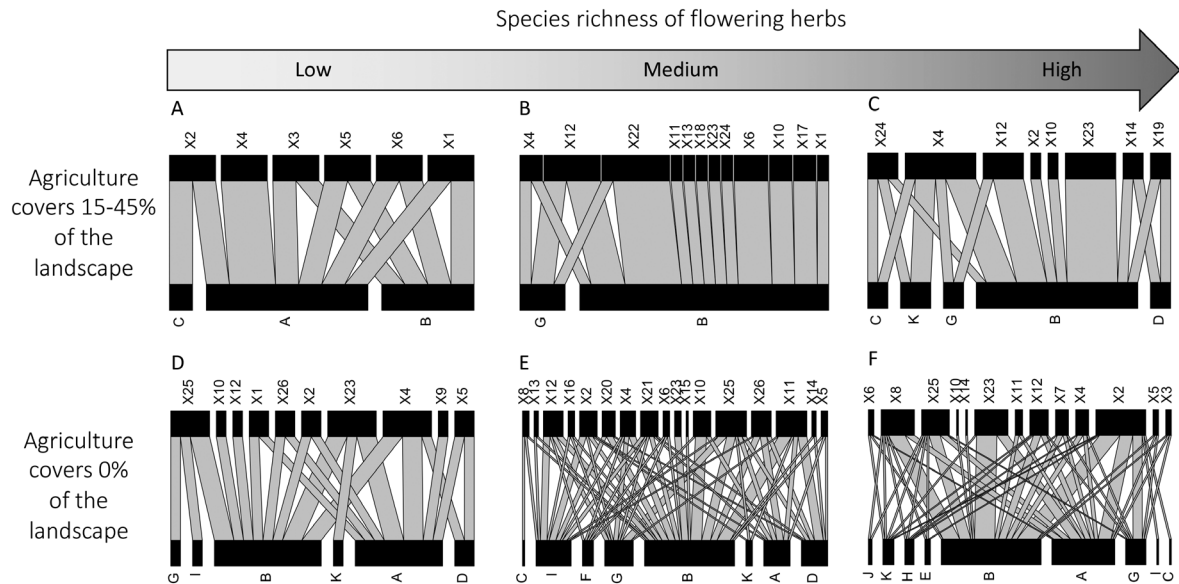


Fig. 3. Network interaction webs for natural enemy (top blocks) and herbivore families (bottom blocks) found on *Brassica oleracea* plants in three urban gardens with agriculture in the urban landscape (A, B, C) or devoid of agriculture in the urban landscape (D, E, F). Interaction webs within each landscape type are situated along a gradient of floral richness of herbaceous plants. Gray bars show links present in a particular site and the width of the gray bar shows the relative frequency with which natural enemy and herbivore families co-occurred in that garden. Natural enemy families encountered were X1, Anthocoridae; X2, Araneae (unidentified family); X3, Araneidae; X4, Braconidae; X5, Clubionidae; X6, Coccinellidae; X7, Encyrtidae; X8, Entelgynae; X9, Eutichuridae; X10, Figitidae; X11, Formicidae; X12, Hymenoptera (unidentified parasitoid family); X13, Ichneumonidae; X14, Linyphiidae; X15, Mymaridae; X16, Nabidae; X17, Neuroptera (unidentified family); X18, Orbicularia; X19, Reduviidae; X20, Salticidae; X21, Scelionidae; X22, Staphylinidae; X23, Syrphidae; X24, Tetragnathidae; X25, Theridiidae; and X26, Vespidae. Herbivore families encountered were A, Aleyrodidae; B, Aphididae; C, Chrysomelidae; D, Cicadellidae; E, Elateridae; F, Hemiptera (unidentified family); G, Lepidoptera (unidentified family); H, Miridae; I, Pentatomidae; J, Pieridae; and K, Thysanoptera (unidentified family).

without agriculture in the landscape, urban cover was not an important predictor of any measures of abundance or network metrics. Across many other studies in the study region, agricultural cover had not been identified as a driver of natural enemy or herbivore abundance (Otoshi et al. 2015, Egerer et al. 2017b, Philpott and Bichier 2017). In this study, however, we focused on arthropods on a single plant species (*B. oleracea*), rather than a more general survey of the community across the gardens, and cole crops such as *B. oleracea* are a major agricultural crop in the study region. Moreover, in the study region, agriculture consists largely of intensively managed, high agrochemical input monocultures of strawberry, cole crop, and lettuce (Letourneau and Bothwell 2008, Chaplin-Kramer et al. 2011, Olimpi and Philpott 2018, Gonthier et al. 2019). In rural agricultural landscapes, landscape-level intensification resulting in habitat loss and fragmentation can negatively impact beneficial insects (Tscharntke et al. 2005). Likewise, the movement and colonization of insect and arthropod populations is negatively affected by fragmentation (McKinney 2002, 2008, Faeth et al. 2005, Williams 2009). Higher amounts of agricultural cover in the landscape could thus deplete natural enemy communities in urban gardens, thereby potentially lowering interaction

richness and vulnerability. Alternatively, natural enemies could be drawn away from urban gardens and into the agricultural fields, if the latter have a higher abundance of host or prey species (Root 1973).

An important and open management question is whether any observed changes in the natural enemy community or network metrics might influence pest suppression services within urban agroecosystems. Answering this question is important because ecosystem services provided by mobile insects (such as parasitoids and predators) are valued in billions of dollars in both rural (Losey and Vaughan 2006) and urban agroecosystems (Clinton et al. 2018). Although we did not measure pest control or plant damage in this study, some of the results on shifts in network metrics associated with local and landscape factors could provide information on potential pest suppression (see for example Philpott and Bichier 2017, Egerer et al. 2020). We found that trophic complementarity, which is predicted to negatively impact pest control, increased with agricultural cover. Specifically, previous studies suggest that networks with lower trophic complementarity, or fewer shared natural enemies per herbivore, should demonstrate higher pest control function either due to more efficient resource use by non-shared predators or apparent competition (Poisot

et al. 2013). Further, Peralta et al. (2014) examined functional complementarity and redundancy in host-parasitoid networks in temperate forests and found that, although high functional complementarity in host use (i.e., few shared host species for each parasitoid) resulted in higher parasitism rates, functional complementarity did not shift with forest structure or type. In another study within this same system, we found that vegetation complexity both enhanced and hindered removal of different prey species (Philpott and Bichier 2017). Specifically, a higher number of trees and shrubs augmented removal of sentinel corn earworm eggs and pea aphids but deterred removal of cabbage looper larvae, and increases in herbaceous plant richness hindered aphid removal (Philpott and Bichier 2017). In addition, increases in agriculture in the landscape negatively affected cabbage worm larvae removal (Philpott and Bichier 2017). Thus some of the same factors that influence network metrics also influence pest control in urban agroecosystems. However, Tylianakis et al. (2007) found that although differences in tropical agroecosystem type had little effect on species richness of natural enemies, highly modified habitats (pasture and rice) supported food webs with higher vulnerability and increased parasitism rates, perhaps due to higher predator or parasitoid search efficiency in simplified habitats (reviewed in Tylianakis and Morris 2017).

Future directions

We provide an important first step toward establishing how antagonistic trophic networks respond to local and landscape management of urban agroecosystems. Future studies could take on two different approaches beyond co-occurrence data for a more specific understanding of natural enemy and herbivore feeding links. First, establishing networks of host–parasitoid interactions could be easily accomplished by collecting *Brassica* herbivores (e.g., aphid mummies, Lepidoptera eggs, larvae, and pupae, Hemiptera eggs) and maintaining those herbivores in the lab to rear parasitoids. Second, diet links for both herbivore parasitoids and predators can be more carefully and specifically established with molecular methods such as metabarcoding validated with qPCR (De Barba et al. 2014, Derocles et al. 2015, Macias-Hernandez et al. 2018). Another limitation of the study, and a long-established phenomenon in predation studies, is that we did not consider intraguild predation or competition between species in the network. However, some of these interactions may certainly explain the patterns that we find and presumed relationships with predation services. Our networks also do not take into account indirect effects or trait-mediated effects, which can be highly influential in agroecosystems (Golubski et al. 2016). These additional approaches, the clearer establishment of host–parasitoid relationships, the molecular analysis of predator and parasitoid diets to build natural-enemy: herbivore networks, and the examination of intraguild

predation or competition among predator species, are ripe areas for future research in urban and other agroecosystems.

In sum, urban gardens are model systems to investigate the mechanistic links between the environment, biodiversity, and delivery of ecosystem services because of their high local management heterogeneity, differences in landscape context, and ability to support valuable ecosystem services. It is critical to understand ecological interactions and networks involving natural enemies and herbivores in urban agroecosystems because arthropods can cause substantial damage to urban crops and cultivated plants (Gregory et al. 2016) but also provide pest control services (Peisley et al. 2015). Applying agroecological principles to maximize productivity and resilience of urban farms will include managing urban agroecosystems and surrounding landscapes to optimize arthropod-mediated ecosystem services (Altieri and Nicholls 2018), which, in turn, requires detailed knowledge of the drivers arthropod community composition and interactions in urban landscapes. Although the effects of some local factors on natural enemies may be context dependent (Egerer et al. 2017a), we show that floral resources and vegetation complexity within urban agroecosystems positively affect natural enemy diversity and abundance, and can also shift network metrics that are connected to increased pest control. Thus, as indicated by studies of habitat manipulations in urban agroecosystems (Altieri and Nicholls 2018, Egerer et al. 2018a), gardeners should be able to manipulate local habitats by increasing floral species richness and vegetation complexity for the benefit of natural enemies and the services that they provide.

ACKNOWLEDGMENTS

We thank H. Cohen, Z. Jordan, T. Milz, Y. Byun, C. Sanchez, J. Tan, and M. Otoshi with assistance with vegetation and landscape data collection. M. Hash identified the spiders. We thank the following gardens and organizations for allowing us to conduct research on site: City of San Jose Parks and Recreation (Berryessa, Coyote Creek, Guadalupe, El Jardín at Emma Prusch Park, Green Thumb, La Colina, Laguna Seca), Charles Street Garden of Sunnyvale, Mid County Senior Center, Aptos Community Garden, Live Oak Grange, City of Santa Cruz (Beach Flats, Trescony), Mesa Verde Gardens (Pajaro, Valle Verde, Mi Jardín Verde), Homeless Garden Project, Center for Agroecology and Sustainable Food Systems Chadwick Garden, MEarth at Carmel Valley Middle School, Our Green Thumb Garden at Middlebury Institute for International Studies, Salinas Community Garden at St. George's Episcopal Church, Chinatown Community Garden, Goodwill Garden of Marina, and Pacific Grove Community Garden. Funding for this project was provided by University of California and USDA-NIFA grant #2016-67019-25185 to S. M. Philpott, B. Lin, S. Jha, and H. Liere.

LITERATURE CITED

Alig, R. J., J. D. Kline, and M. Lichtenstein. 2004. Urbanization on the US landscape: looking ahead in the 21st century. *Landscape and Urban Planning* 69:219–234.

- Almeida-Neto, M., P. Guimarães, P. R. Guimarães, R. D. Loyola, and W. Ulrich. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117:1227–1239.
- Altieri, M. A., and C. I. Nicholls. 2018. Urban Agroecology: designing biodiverse, productive and resilient city farms. *Agro Sur* 46:49–60.
- Andow, D. 1991. Vegetational diversity and arthropod population response. *Annual Review of Entomology* 36:561–586.
- AphID. 2017. <http://aphid.aphidnet.org/>
- Barton, K. 2012. MuMin: Multi-model inference. R package version 1.5.2. <http://CRAN.R-project.org/package=MuMin>
- Bascompte, J., P. Jordano, C. J. Melian, and J. M. Olesen. 2003. The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences USA* 100:9383–9387.
- Bell, J. R., R. A. King, D. A. Bohan, and W. O. C. Symondson. 2010. Spatial co-occurrence networks predict the feeding histories of polyphagous arthropod predators at field scales. *Ecography* 33:64–72.
- Bennett, A. B., and C. Gratton. 2012. Local and landscape scale variables impact parasitoid assemblages across an urbanization gradient. *Landscape and Urban Planning* 104:26–33.
- Bersier, L.-F., C. Banašek-Richter, and M.-F. Cattin. 2002. Quantitative descriptors of food-web matrices. *Ecology* 89:2394–2407.
- Bianchi, F. J., C. J. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B* 273:1715–1727.
- Bluthgen, N. 2010. Why network analysis is often disconnected from community ecology: a critique and an ecologist's guide. *Basic and Applied Ecology* 11:185–195.
- Blüthgen, N., F. Menzel, T. Hovestadt, B. Fiala, and N. Bluthgen. 2007. Specialization, constraints, and conflicting interests in mutualistic networks. *Current Biology* 17:341–346.
- Bohan, D. A., et al. 2013. Networking Agroecology: integrating the diversity of agroecosystem interactions. Pages 1–67 in G. Woodward, and Bohan, D. A. editors. *Advances in ecological research*. Volume 49: Ecological networks in an agricultural world. Elsevier, Oxford, UK
- Borror, D. J., and R. E. White. 1970. *A field guide to insects: America north of Mexico*. Houghton Mifflin Harcourt, Boston, Massachusetts, USA.
- Breheny, P., and W. Burchett. 2013. Visualization of regression models using visreg. *R Journal* 9:56–71.
- Brown, K., and A. Jameton. 2000. Public health implications of urban agriculture. *Journal of Public Health Policy* 21:20–39.
- BugGuide. 2017. <https://bugguide.net/node>
- Burkman, C., and M. Gardiner. 2014. Urban greenspace composition and landscape context influence natural enemy community composition and function. *Biological Control* 75:58–67.
- Burks, J. M., and S. M. Philpott. 2016. Local and landscape drivers of parasitoid abundance, richness, and composition in urban gardens. *Environmental Entomology* 46:201–209.
- Calcagno, V., and C. de Mazancourt. 2010. glmulti: an R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software* 34:1–29.
- Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443:989–992.
- Chaplin-Kramer, R., M. E. O'Rourke, E. J. Blitzer, and C. Kremen. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters* 14:922–932.
- Chappell, M., and L. LaValle. 2011. Food security and biodiversity: can we have both? An agroecological analysis. *Agriculture and Human Values* 28:3–26.
- Classens, M. 2015. The nature of urban gardens: toward a political ecology of urban agriculture. *Agriculture and Human Values* 32:229–239.
- Clinton, N., M. Stuhlmacher, A. Miles, N. U. Aragon, M. Wagner, M. Georgescu, C. Herwig, and P. Gong. 2018. A global geospatial ecosystem services estimate of urban agriculture. *Earth's Future* 6:40–60.
- Colding, J., J. Lundberg, and C. Folke. 2006. Incorporating green-area user groups in urban ecosystem management. *Ambio* 35:237–244.
- De Barba, M., C. Miquel, F. Boyer, C. Mercier, D. Rioux, E. Coissac, and P. Taberlet. 2014. DNA metabarcoding multiplexing and validation of data accuracy for diet assessment: application to omnivorous diet. *Molecular Ecology Resources* 14:306–323.
- Delgado de la Flor, Y. A., C. E. Burkman, T. K. Eldredge, and M. M. Gardiner. 2017. Patch and landscape-scale variables influence the taxonomic and functional composition of beetles in urban greenspaces. *Ecosphere* 8:e02007.
- Derocles, S. A. P., D. M. Evans, P. C. Nichols, S. A. Evans, and D. H. Lunt. 2015. Determining plant-leaf miner-parasitoid interactions: a DNA barcoding approach. *PLoS ONE* 10: e0117872.
- Devoto, M., S. Bailey, P. Craze, and J. Memmott. 2012. Understanding and planning ecological restoration of plant-pollinator networks. *Ecology Letters* 15:319–328.
- Dormann, C. F., B. Gruber, and J. Fründ. 2008. Introducing the bipartite Package: Analysing Ecological Networks. *R News* 8:8–11.
- Egerer, M. H., C. Arel, M. D. Ootshi, R. D. Quistberg, P. Bichier, and S. M. Philpott. 2017a. Urban arthropods respond variably to changes in landscape context and spatial scale. *Journal of Urban Ecology* 3:1–10.
- Egerer, M. H., P. Bichier, and S. M. Philpott. 2017b. Landscape and local habitat correlates of lady beetle abundance and species richness in urban agriculture. *Annals of the Entomological Society of America* 110:97–103.
- Egerer, M. H., H. Liere, P. Bichier, and S. M. Philpott. 2018a. Cityscape quality and resource manipulation affect natural enemy biodiversity in and fidelity to urban agroecosystems. *Landscape Ecology* 33:985–998.
- Egerer, M. H., H. Liere, B. B. Lin, S. Jha, P. Bichier, and S. M. Philpott. 2018b. Herbivore regulation in urban agroecosystems: direct and indirect effects. *Basic and Applied Ecology* 29:44–54.
- Egerer, M. H., H. Liere, A. Lucatero, and S. M. Philpott. 2020. Plant damage in urban agroecosystems varies with local and landscape factors. *Ecosphere* 11:e03074.
- Fabian, Y., N. Sandau, O. T. Bruggisser, A. Aebi, P. Kehrl, R. P. Rohr, R. E. Naisbit, and L. F. Bersier. 2013. The importance of landscape and spatial structure for hymenopteran-based food webs in an agro-ecosystem. *Journal of Animal Ecology* 82:1203–1214.
- Faeth, S. H., W. A. Marussich, E. Shochat, and P. S. Warren. 2005. Trophic dynamics in urban communities. *BioScience* 55:399.
- Fox, J., and S. Weisberg. 2011. *An R companion to applied regression*. Second edition. Sage, Thousand Oaks, California, USA.
- Gagic, V., S. Hänke, C. Thies, C. Scherber, Ž. Tomanović, and T. Tscharntke. 2012. Agricultural intensification and cereal aphid-parasitoid-hyperparasitoid food webs: network complexity, temporal variability and parasitism rates. *Oecologia* 170:1099–1109.

- Gardiner, M. M., S. P. Prajzner, C. E. Burkman, S. Albro, and P. S. Grewal. 2014. Vacant land conversion to community gardens: influences on generalist arthropod predators and biocontrol services in urban greenspaces. *Urban Ecosystems* 17:101–122.
- Golubski, A. J., E. E. Westlund, J. Vandermeer, and M. Pascual. 2016. Ecological networks over the edge: hypergraph trait-mediated indirect interaction (TMII) structure. *Trends in Ecology & Evolution* 31:344–354.
- Gonthier, D. J., A. R. Sciligo, D. S. Karp, A. Lu, K. Garcia, G. Juarez, T. Chiba, S. Gennet, and C. Kremen. 2019. Bird services and disservices to strawberry farming in Californian agricultural landscapes. *Journal of Applied Ecology* 56:1948–1959.
- Gregory, M. M., T. W. Leslie, and L. E. Drinkwater. 2016. Agroecological and social characteristics of New York city community gardens: contributions to urban food security, ecosystem services, and environmental education. *Urban Ecosystems* 19:763–794.
- Griffith, G. E., J. M. Omernik, D. W. Smith, T. D. Cook, E. Talyn, K. Moseley, and C. B. Johnson. 2016. Ecoregions of California. USGS Numbered Series. U.S. Geological Survey, Reston, Virginia, USA.
- Hodgson, K., M. Campbell, and M. Bailkey. 2011. *Urban agriculture: Growing healthy, sustainable places*. American Planning Association, Chicago, IL.
- Homer, C., J. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. Herold, J. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States—representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing* 81:345–354.
- Ings, T. C., et al. 2009. Ecological networks—beyond food webs. *Journal of Animal Ecology* 78:253–269.
- Jordano, P. 2016. Sampling networks of ecological interactions. *Functional Ecology* 30:1883–1893.
- Laliberté, E., and J. M. Tylianakis. 2010. Deforestation homogenizes tropical parasitoid—host networks homogenizes tropical parasitoid—host. *Ecology* 91:1740–1747.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45:175–201.
- Langellotto, G. A., and R. F. Denno. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* 139:1–10.
- Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16:545–556.
- Letourneau, D. K., and S. G. Bothwell. 2008. Comparison of organic and conventional farms: challenging ecologists to make biodiversity functional. *Frontiers in Ecology and the Environment* 6:430–438.
- Liere, H., M. H. Egerer, and S. M. Philpott. 2019. Environmental and spatial filtering of ladybird beetle community composition and functional traits in urban landscapes. *Journal of Urban Ecology* 5.
- Lin, B. B., S. M. Philpott, and S. Jha. 2015. The future of urban agriculture and biodiversity-ecosystem services: challenges and next steps. *Basic and Applied Ecology* 16:189–201.
- Losey, J. E., and M. Vaughan. 2006. The economic value of ecological services provided by insects. *BioScience* 56:311–323.
- Macias-Hernandez, N., K. Athey, V. Tonzo, O. S. Wangenstein, M. Arnedo, and J. D. Harwood. 2018. Molecular gut content analysis of different spider body parts. *PLoS ONE* 13: e0196589.
- Marshall, S. A. 2006. *Insects: their natural history and diversity: with a photographic guide to insects of Eastern North America*. Firefly Books, Richmond Hill, Ontario, Canada.
- McGarigal, K., S. Cushman, M. Neel, and E. Ene. 2002. FRAGSTATS v3: spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst, Massachusetts, USA. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- McKinney, M. L. 2002. Urbanization, Biodiversity, and Conservation The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience* 52:883–890.
- McKinney, M. L. 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems* 11:161–176.
- Oberholtzer, L., C. Dimitri, and A. Pressman. 2014. Urban agriculture in the United States: characteristics, challenges, and technical assistance needs. *Journal of Extension* 52:6FEA1.
- Oksanen, J., et al. 2018. *Vegan: community ecology package*. R package version 2.3-4. <http://CRAN.R-project.org/package=vegan>
- Olimpi, E. M., and S. M. Philpott. 2018. Agroecological farming practices promote bats. *Agriculture, Ecosystems & Environment* 265:282–291.
- Otoshi, M., P. Bichier, and S. M. Philpott. 2015. Local and landscape correlates of spider activity density and species richness in urban gardens. *Environmental Entomology* 44:1043–1051.
- Peisley, R. K., M. E. Saunders, and G. W. Luck. 2015. A Systematic review of the benefits and costs of bird and insect activity in agroecosystems. *Springer Science Reviews* 3:113–125.
- Peralta, G., C. M. Frost, T. A. Rand, R. K. Didham, and J. M. Tylianakis. 2014. Complementarity and redundancy of interactions enhance attack rates and spatial stability in host-parasitoid food webs. *Ecology* 95:1888–1896.
- Perović, D. J., S. Gamez-Virues, D. A. Landis, F. Wackers, G. M. Gurr, S. D. Wratten, M. S. You, and N. Desneux. 2018. Managing biological control services through multi-trophic trait interactions: review and guidelines for implementation at local and landscape scales. *Biological Reviews* 93:306–321.
- Perrings, C., et al. 2010. Ecosystem services for 2020. *Science* 330:323–324.
- Philpott, S. M., et al. 2008. Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. *Conservation Biology* 22:1093–1105.
- Philpott, S. M., S. Albuquerque, P. Bichier, H. Cohen, M. H. Egerer, C. Kirk, and K. W. Will. 2019. Local and landscape drivers of carabid activity, species richness, and traits in urban gardens in Coastal California. *Insects* 10:112.
- Philpott, S. M., and P. Bichier. 2017. Local and landscape drivers of predation services in urban gardens. *Ecological Applications* 27:966–976.
- Poisot, T., N. Mouquet, and D. Gravel. 2013. Trophic complementarity drives the biodiversity-ecosystem functioning relationship in food webs. *Ecology Letters* 16:853–861.
- Pothukuchi, K., and B. Thomas. 2004. Food deserts and access to retail grocery in inner cities. *Community News & Views* 17:6–7.
- R Development Core Team. 2018. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>

- Raupp, M. J., P. M. Shrewsbury, and D. A. Herms 2010. Ecology of herbivorous arthropods in urban landscapes. *Annual Review of Entomology* 55:19–38.
- Rodewald, A. D., R. P. Rohr, M. A. Fortuna, and J. Bascompte. 2015. Does removal of invasives restore ecological networks? An experimental approach. *Biological Invasions* 17:2139–2146.
- Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95–124.
- Schleuning, M., J. Frund, and D. Garcia. 2015. Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant-animal interactions. *Ecography* 38:380–392.
- Smit, J., J. Nasr, and A. Ratta 1996. Urban agriculture: food, jobs and sustainable cities. The Urban Agriculture Network, Inc., New York, New York, USA.
- Thompson, R. M., et al. 2012. Food webs: reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution* 27:689–697.
- Tscharntke, T., Y. Clough, T. C. Wanger, L. Jackson, I. Motzke, I. Perfecto, J. Vandermeer, and A. Whitbread. 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation* 151:53–59.
- Tscharntke, T., A.-M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecology Letters* 8:857–874.
- Tylianakis, J. M., and A. Binzer. 2014. Effects of global environmental changes on parasitoid-host food webs and biological control. *Biological Control* 75:77–86.
- Tylianakis, J. M., E. Laliberte, A. Nielsen, and J. Bascompte. 2010. Conservation of species interaction networks. *Biological Conservation* 143:2270–2279.
- Tylianakis, J. M., and R. J. Morris. 2017. Ecological networks across environmental gradients. *Annual Review of Ecology, Evolution, and Systematics* 48:25–48.
- Tylianakis, J. M., T. Tscharntke, and O. T. Lewis. 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature* 445:202–205.
- UC IPM. 2017. <http://ipm.ucanr.edu/>
- Ver Ploeg, M., et al. 2009. Access to affordable and nutritious food: measuring and understanding food deserts and their consequences. Report to Congress. U.S. Department of Agriculture, Washington, D.C.
- Williams, M. R. 2009. Butterflies and day-flying moths in a fragmented urban landscape, south-west Western Australia: patterns of species richness. *Pacific Conservation Biology* 15:32–46.
- Woodward, G., and D. Bohan 2013. Ecological networks in an agricultural world. First edition. Academic Press, Washington, D.C., USA.
- Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media, New York, New York, USA.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2201/full>

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: <https://doi.org/10.7291/D1DH3N>