UNIVERSITY OF CALIFORNIA
SANTA CRUZ

ECOLOGICAL COMPLEXITY AND SOCIO-ECOLOGICAL INTERACTIONS IN URBAN AGROECOSYSTEMS

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY in

ENVIRONMENTAL STUDIES

By

Azucena Lucatero

June 2023

The Dissertation of Azucena Lucatero is approved:

Professor Stacy M. Philpott, chair

Professor Madeleine Fairbairn

Professor Christopher Wilmers

Peter Biehl
Vice Provost and Dean of Graduate Studies

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

ECOLOGICAL COMPLEXITY AND SOCIO-ECOLOGICAL INTERACTIONS IN URBAN AGROECOSYSTEMS

Azucena Lucatero

Ecological complexity supports biodiversity, robust community structure, and resilient ecosystem functions. In agroecosystems, adding ecological complexity by diversifying crops and agricultural landscapes can help foster complex webs of relationships between pests and their natural enemies that leads to enhanced biological pest control. Urban community gardens provide a unique opportunity to investigate how differences in human management and urban landscapes affect the insect biodiversity, species interactions, and ecosystem services that support food production in urban settings. In my dissertation, I investigate various forms and scales of ecological complexity in community gardens of the California central coast to understand the social and ecological processes that give rise to this complexity as well as its implications for biological pest control in urban agriculture. First, I quantify ecological complexity at the local scale of individual gardener plots by measuring the density, diversity, and connectivity of plot vegetation and its impacts on garden herbivores and natural enemies (Chapter 1). Next, I use ecological networks of interactions between pests and parasitoid wasps to measure changes in pest–parasitoid interactions along gradients of local garden management and landscape composition (Chapter 2). Additionally, I examine the metacommunity structure of herbivores and natural enemies inhabiting urban gardens in the study region and identify garden habitat and landscape characteristics that influence arthropod metacommunity structure (Chapter 3). Finally, I examine how differences in gardener aesthetic norms and management priorities lead to variation in ecological complexity in community gardens (Chapter 4). In line with agroecological theory, this work finds that higher amounts of ecological complexity support greater natural enemy diversity and higher rates of pest parasitism. While common preferences for "tidiness" may limit ecological complexity in some garden plots, gardeners who prioritize "wildness" in their plots present viable alternatives for garden management that help to diversify the ecological habitat and resources provided by community gardens.

DEDICATION

To my parents,

and to all the teachers, professors, mentors, and friends

who supported me along the way.

ACKNOWLEDGEMENTS

The story of this dissertation begins with my parents, Maria Castañeda and Javier Lucatero. Without their many personal sacrifices and constant encouragement of my educational pursuits, I would not be here today. Many academics joke that their families don’t know or understand what they do. But it has been important for me to communicate to my parents the work and opportunities I have been privileged to undertake, thanks in no small part to them. Over many phone calls, I have endeavored to translate my experiences in the academy for my parents to the best of my ability. Very often, my mother gave excellent advice about whatever academic dilemma I was facing. My parents have been among my biggest cheerleaders and most ardent supporters throughout my studies. The achievements represented by this completed dissertation are theirs, too. Like many immigrant mothers, my mother always hoped that I would become a doctor. I suppose I fulfilled her wish in my own way. Of course, I also owe a lot of gratitude to my partner, Holden Parks. We started graduate school at about the same time but on opposite coasts, and we have supported each other through all the ups and downs of this academic journey. Thank you for the near daily calls, the cross-country visits, and for helping me out with a whole week of intense field work during one of those summer visits. I also thank my brother, Christian Lucatero, for looking after our parents while I’ve been gone, helping me move, doing some lab work with me, and taking lots of great photographs. And thanks to my cats, Nube and Sora, for brightening my life and keeping me company.

I’m immensely grateful to all the academic mentors and colleagues who helped make this dissertation possible. First, my PhD advisor, Stacy Philpott. Thank you for your patient mentorship, for fostering a wonderful lab community, and for modeling rigorous and critical approaches to science. I thank my committee members, Madeleine Fairbairn and Chris Wilmers, for their constructive feedback, advice, and overall efforts to get me through my PhD milestones. I extend deep gratitude to my undergraduate mentors, Theresa Ong and Liz Vallen, for believing in me and helping me get to graduate school in the first place. I also acknowledge my fantastic ANTS lab and BUGS project colleagues: Hamutahl Cohen, Monika Egerer, Edith Gonzales, Suzanne Lipton, Sanya Cowal, Clara Qin, Peter Bichier, Heidi Liere, Shalene Jha, Brenda Lin, and many undergraduate researchers. I’m grateful for the support of my ENVS cohort mates, especially Justin Luong, Aysha Peterson, and Allyson Makuch. Thank you also to the many informal peer mentors I met through AAHHE, the Ford Foundation, the Community Engaged Research Institute, and other academic community spaces, for encouraging me and helping me navigate the often difficult to read landscape of academia.

I would not have been able to make it through this graduate program without the steadfast support of many dear friends. Thank you to the UCSC Women Center’s MINT program, where I met Kiki Rosales and immediately gained a brilliant friend and huge role model for leading social justice in academia and beyond. Thank you to all my MINT mentees, especially my first mentee, Luz Ticas, for the mutual support and care. Special thanks to my adoptive cohort in the Psychology department, especially Brenda Gutierrez, Paulette Garcia Peraza, and Ibette Valle. I’m eternally grateful for the fateful day that led me to you all and for the friendship and solidarity you so generously shared with me over the years. You made me feel seen and understood in an environment where I often felt the opposite, and you helped me find the strength to keep going when I wanted to give up. The four of us went on to form the Women of Color Graduate Community Group, which was a great source of mutual support, advice, and joy for me. I would also like to thank my friends outside of the academy, Quetzal Ramirez, Taylor Tai, Antonio Mendoza, Lindsy Hockenberry, Karla Verdin, and Yesenia Garcia, for listening to all my graduate school chisme, offering moral support, and helping to keep me sane and grounded.

Finally, I would like to thank the bugs. I often credit the ladybugs, aphids, earthworms, snails, and butterflies I encountered on my elementary school’s grassy field and my mother’s rose garden with starting me down the path that eventually led to my graduate studies. I never would have thought I would become a bug person so many years later. Thank you for inspiring wonder, fascination, and many questions.

This dissertation took place on the unceded territories of the Amah Mutsun, Esselen, and Muwekma Ohlone Tribal Bands. This work was funded by the Chicana Latina Foundation scholarship, many Heller Agroecology grants, the Chancellor’s Graduate Internship, the Ford Foundation Predoctoral Fellowship, the UC Global Food Initiative, the Chancellor’s Dissertation Year Fellowship, and the UCSC Environmental Studies department. Thank you to all the urban gardeners who allowed me to conduct research at their sites and who participated in my dissertation.

CHAPTER 1: Local habitat complexity and its effects on garden herbivores and natural enemies

Abstract

Habitat complexity generally supports biodiversity and is an important element of biological pest control strategies in agroecosystems. In urban community gardens, the cultivated vegetation in gardener plots provides variable levels of habitat complexity, which can suppress pests by promoting a diversity of natural enemies and improving pest control. In this study, we examine three components of the structural complexity of urban garden vegetation (density, diversity, and connectivity) to investigate whether higher garden vegetation complexity leads to fewer herbivores, more natural enemies, and higher pest control levels. We worked in 8 community gardens in the California central coast to quantify vegetation complexity, sample the arthropod community using visual surveys and pitfall traps, and measure predation levels using sentinel pest experiments. We found that gardener plots with high vegetation density supported a greater richness of foliage-dwelling natural enemies and a greater abundance of ground-dwelling natural enemies. High vegetation density also supported a greater abundance and richness of spiders on foliage. High vegetation diversity was negatively associated with the abundance of natural enemies at the ground-level, although this result may track a shift in ant foraging activity from the ground to plot foliage under high vegetation diversity. None of our vegetation complexity metrics predicted herbivore abundance and richness or predation in sentinel pest experiments. While high natural enemy abundance was positively

associated with egg predation, greater species diversity of natural enemies had a negative impact on egg predation, suggesting that antagonism between natural enemies may limit biological control. Thus, community gardeners may be able to manipulate vegetation density and diversity at the small scale of their individual garden plots to promote a greater abundance and diversity of natural enemies on their crops. However, the species composition of natural enemy species and the prevalence of interspecific antagonism may ultimately determine subsequent impacts on biological pest control.

Introduction

The complexity of a habitat is an important factor determining the distribution and diversity of species. Habitat complexity describes the heterogeneity of biotic and abiotic components in an ecosystem. Measurements of habitat complexity vary according to the specific components being considered, but the structure and diversity of topography, substrates, and vegetation are frequently used as proxies (Kovalenko et al. 2012, Loke and Chisholm 2022). Ecological observations have often linked habitat complexity with greater species diversity and abundance in both aquatic and terrestrial systems (MacArthur 1965, Pianka 1966, August 1983, Dean and Connell 1987, St. Pierre and Kovalenko 2014, Badgley et al. 2017). High habitat complexity conferred by heterogenous vegetation and ground cover can provide a variety of microhabitats and microclimates, supporting a greater variety of species functional groups and foraging habits in arthropods (Uetz 1979, Lassau et al. 2005). The structural complexity of vegetation can also act as an environmental filter shaping assemblages of arthropod species and their functional traits (Nooten et al. 2019). Additionally, structurally complex habitats can provide refuges and facilitate resource partitioning that supports the coexistence of predator and prey species as well as multiple competing predators in a system (Huffaker 1958, Finke and Denno 2002).

In agroecosystems, adding habitat complexity by diversifying crops and agricultural landscapes can promote the natural enemies of pests, leading to enhanced biological pest control (Chaplin-Kramer and Kremen 2012, Gurr et al. 2017, He et al. 2019). Conventional agricultural practices typically produce simplified, monocultural habitats that often rely on pesticides to combat pest outbreaks (Meehan et al. 2011, Nicholson and Williams 2021). In contrast, agroecological approaches to pest control emphasize biological diversification as a means of controlling pests (Altieri et al. 1983, Wezel et al. 2014, Ong and Liao 2020). Ecological theory proposes several explanatory mechanisms. First, herbivores accumulate at high densities in monoculture plantings because of resource concentration of their preferred host plants (Root 1973). Crop diversification can therefore disrupt herbivorous pests by preventing pests from finding host plants and reduces pest densities through bottom-up regulation (Letourneau et al. 2011). Second, crop diversification can also facilitate pest suppression through top-down regulation. According to the enemies hypothesis, complex habitats provide a variety of microhabitats, prey species, and alternative resources that support a greater diversity and abundance of natural enemy species (Root 1973). In turn, a high diversity of natural enemies can result in greater pest suppression due to niche complementarity, whereby diverse natural enemy communities target different prey species or exploit different locations and thus consume more pests than assemblages with fewer natural enemies (Duffy 2002, Ives et al. 2005). Empirical study of the relationship between habitat complexity and natural enemies generally supports the enemies hypothesis (Russell 1989, Redlich et al. 2018, González-Chang et al. 2019). For instance, a metanalysis examining 43 studies found that habitats with high vegetation and ground cover complexity supported a higher abundance of natural enemies of several different taxa in seven out of nine guilds (Langellotto and Denno 2004). More recently, a study of European vineyards found that including more cover crop species increased the abundance of natural enemies, but crop diversity only had positive effects on predation rates in simple landscapes as opposed to complex landscapes (Beaumelle et al. 2021). However, studies of the subsequent impacts of habitat complexity on pest control are less common and deserve further investigation.

A key element of habitat complexity with consequences for biological pest control is vegetation complexity, which consists of several components that can each influence arthropods in distinct ways. First, plant species composition has received a great deal of attention in the ecological literature, with synthetic reviews of both rural and urban systems finding that plant diversity often promotes natural enemy diversity (Letourneau et al. 2011, Burkman and Gardiner 2014). As addressed by the enemies hypothesis above, plant species richness can benefit natural enemies through provision of diverse habitat and resources. More plant species also contributes diverse plant volatiles, the secondary metabolites emitted by plants in response to herbivory to recruit natural enemies via chemical signaling, although the interacting effects of volatiles from multiple plants are still under study (Randlkofer et al. 2010b). However, plant diversity effects on natural enemies can be species specific or depend on arthropod traits like size, diet breadth, and mobility (Thomson and Hoffmann 2010, Moreira et al. 2016). A second component of vegetation complexity is the architectural structure of individual plants, including plant vertical height, branching structures, and the size and shape of leaves and flowers (Lawton 1983). Plant architectural features can affect arthropod mobility, search efficiency and foraging success, and mortality with consequences for pest control (Marquis et al. 1996, Inbar and Gerling 2008, Obermaier et al. 2008). For example, a study of four cruciferous plant architectures observing the foraging behaviors of predatory beetles found that variation in plant shape, texture, and surface area affected beetle foraging success by altering ease of movement, frequency of falling from the plant, and ability to reach aphids (Grevstad and Klepetka 1992). In some instances, architectural structures improved beetle grip on leaves as they foraged, while in others architectural structures provided refugia for aphid herbivores from natural enemies. Plant architectural structures may thus alternately advantage herbivores and natural enemies, making it important to understand the exact conditions that favor natural enemy foraging success to inform agroecosystem management. Third, the connectivity of plants, or the spatial arrangement and overlap of plants relative to each other, similarly affects how arthropods navigate habitats. One greenhouse study of ladybeetles on bean plants observed that ladybeetles traveled further in treatments with high leaf overlap, suggesting that high connectivity between plants may increase predator foraging efficiency (Kareiva and Perry 1989).

In urban settings, habitat complexity is distributed as a mosaic that structures urban biodiversity. Intensive human land use drives habitat loss and fragmentation, but patches of remnant natural habitat and human managed green spaces persist throughout urban landscapes. The patchiness of urban green space habitats lends itself well to the application of island biogeography theory, which predicts that smaller and more isolated patches support fewer species compared to larger, well connected habitat patches (MacArthur and Wilson 1967, Breuste et al. 2008). Plant species richness in particular tends to be high in urban green spaces due to the importation of introduced species by people (Faeth et al. 2011). Surveys of home gardens have found especially elevated numbers of plant species compared to remnant natural and semi-natural urban habitats, with vegetation quadrats in gardens containing over twice as many plant species as any other habitat (Thompson et al. 2003). In contrast, animal species richness tends to decline overall while the abundance of certain taxa, including some arthropods, increases (Faeth et al. 2011, Fenoglio et al. 2020). Patterns of urbanization can further alter the composition of the arthropod community. Arthropod species respond differently to urban habitat heterogeneity, with some being able to exploit small remnant habitat patches while others are more sensitive to habitat size, disturbance, and isolation (McIntyre et al. 2001). Aronson et al. (2016) propose three major hierarchical filters that determine species composition in urban habitats. These are: 1) environmental factors, such as microclimate, biogeography, and land-use, 2) biotic factors, including species interactions, life histories, and traits, and 3) anthropogenic factors of socioeconomics, culture, urban form, and legacies of previous land use. However, the mechanisms underlying shifts in biodiversity in response to these urban filters are not well understood. Hypothesized mechanisms center on species responses to differences in the quality and primary productivity of urban habitat patches as well as cascading competitive and trophic interactions (Shochat et al. 2006).

Urban agroecosystems, such as urban farms and gardens, provide a unique opportunity to investigate the role of habitat complexity on pest control. Urban agroecosystems are dynamic green spaces that provide diverse vegetative structures supporting urban biodiversity and ecosystem service provision (Lin et al. 2015). Among these ecosystem service providers are the natural enemies of pests that provision biological pest control. Biological pest control is a critical ecosystem service in urban agriculture (Gardiner et al. 2013, Nighswander et al. 2021), where the vast majority of urban growers report facing significant challenges in managing crop pests, and often lack the technical knowledge to do so (Oberholtzer et al. 2014). In particular, urban community gardens are well suited to investigating vegetation complexity at the local scale. Community gardens are managed by several gardeners in individual allotment plots which vary in vegetation complexity depending on gardeners’ choice of cultivated plants and management practices like frequency of weeding and pruning (Cabral et al. 2017). Previous work in urban agroecosystems has examined aspects of habitat complexity and its effects on herbivores, natural enemies, and pest control in urban agroecosystems, finding associations with garden characteristics such as garden size, woody vegetation, floral abundance, and ground cover throughout the whole garden (Philpott and Bichier 2017, Lowenstein and Minor 2018, Egerer et al. 2020b). The present study builds on this work by focusing on vegetation complexity and arthropods in individual gardener plots, which is the scale at which gardeners make changes to the vegetation complexity in community gardens and is thus a highly relevant scale to understand for ecological applications in these agroecosystems.

In this study, we quantify vegetation complexity in community garden plots and its subsequent impacts on the arthropod community and predation. We investigate two main questions: 1) Does vegetation complexity at the garden plot-level differentially influence the abundance and richness of herbivores and natural enemies, and 2) How does vegetation complexity affect predation levels provided by natural enemies? Drawing from the resource concentration and enemies hypotheses, we predict that gardens with higher vegetation density will have more herbivores and lower predation levels while gardens with higher vegetation diversity and connectivity will support more natural enemies and enhance predation.

Methods

Study system

This study took place at eight community garden sites in the California central coast (Santa Cruz and Monterey counties) during the summer growing season in 2019 (Aug 1 – 5). Six of the eight garden sites are grown in allotments, dividing the land into parcels assigned to individuals. The remaining two sites are managed collectively by student groups and school personnel. We were limited to these eight sites (out of 30 gardens we have previously studied in the region) because of constraints in recruiting gardeners willing to have their plots intensively sampled for the duration of this study. The garden sites range from 444 m^2 to 6,070 m^2 in size and are separated from each other by at least 2 km. All gardens are organically managed and had been cultivated between 4 and 37 years at the time of the study. Overall, these sites represent a gradient of garden management practices and resultant habitat complexity.

Vegetation and ground cover surveys

At each garden we recruited four gardener plots. We recruited plots that visually appeared to vary in habitat complexity, two with high vegetation complexity (e.g. many plants in the plot) and two with low vegetation complexity (e.g. fewer plants in the plot). We then quantified the vegetation and ground cover in a 1.5 x 1.5 m area of each gardener plot to standardize the sampled area (plots ranged in size from 0.98 m^2 – 70.3 m^2). Within each 1.5 x 1.5 m plot, we identified all plant species, estimated the percent cover of herbaceous and woody vegetation, measured the longest distance between two plants in the plot and the height of the tallest vegetation, counted the number of inflorescences, counted the number of plant species in flower, and estimated the percent non-plant ground cover (i.e. bare soil, grass, rocks, leaf litter, mulch, straw).

Arthropod community surveys

We sampled the arthropod community at each plot twice within three days (on August 1 and August 3). To sample arthropods on plot foliage, we haphazardly placed two 0.25 m x 0.25 m quadrats in each plot. We then visually surveyed the plants in each quadrat by carefully inspecting all plant leaves and structures and recording the abundance and identity of all herbivore and natural enemy species we encountered. We collected all arthropods not readily identifiable in the field and preserved them in 70% ethanol. To sample ground-dwelling arthropods, we placed one pitfall trap in the center of each gardener plot. Pitfall traps consisted of 12 oz. clear plastic containers filled half-way full with saline solution and a drop of detergent. We buried pitfall traps level with the surface of the soil and left traps in each plot for 24 hours. After collecting the pitfall traps, we rinsed arthropod samples in water and preserved them in 70% ethanol. We identified all arthropods to morphospecies using dichotomous keys and online resources (Borror and White 1970, Iowa State University Department of Entomology 2003, Marshall 2006).

Sentinel pest removal experiment

We conducted sentinel pest removal experiments to measure the predation services provided by natural enemies occurring in the study plots. We used potted fava bean (*Vicia faba*) plants grown under greenhouse conditions and inoculated plants with one of two types of sentinel prey: pea aphids (*Acyrthosiphon pisum*) and corn earworm eggs (*Helicoverpa zea*). We purchased aphids from Nasco Education (Fort Atkinson, WI, USA) and eggs from Frontier Agricultural Sciences (Newark, DE, USA) under USDA-Aphis Permit P526P-14-02660. To prepare aphid prey, we reared pea aphids on potted fava bean plants at the UC Santa Cruz Interdisciplinary Sciences Building Greenhouse until aphid populations reached ~600-1200 aphids per plant. To prepare egg prey, we cut the cloth sheets onto which eggs had been laid into 1 cm x 1 cm squares (~600 eggs per square on average) and stored eggs in a freezer prior to field experiments. We randomly assigned egg squares to a site and field treatment, and we photographed all squares with a microscope camera before and after field experiments to count the starting number of eggs and the number of eggs removed during the experiment.

For field experiments, we transported potted fava bean plants to garden sites. Upon arrival, we counted the number of aphids on experimental plants and randomly assigned plants to either an open (predator access) or bagged (predator exclusion) treatment. For egg prey plants, we pinned egg squares onto two leaves of each fava plant, bagging one leaf and leaving the second leaf open. We used mesh paint strainer secured with rubber hair ties for the bagged treatments. We placed one set of fava plants (open aphid, bagged aphid, open/bagged egg) on the perimeter of each gardener plot. After 24 hours, we retrieved plants to recount the number of aphids present and collected egg squares for recounting. Because eggs were frozen prior to the experiment, we assume all eggs were removed by predators and not due to egg eclosion. Recent observations from our system confirm that a variety of arthropod predators, including ants and predatory hemipterans, actively remove egg prey (Philpott, S., unpublished data). We noted whether any predators were present within bags to ensure that predator exclusion treatments were effective.

Data analysis

We calculated three different metrics of vegetation complexity: vegetation density (percent herbaceous cover), vegetation diversity (number of plant species), and vegetation connectivity (1/the longest distance between two plants in a plot). We measured these metrics in an applied setting that did not allow us to experimentally isolate each component of vegetation complexity. In examining Pearson correlation coefficients between our vegetation metrics, we found weak to moderate correlations (R^2 between 0.1 to 0.55; Table 1.1), indicating that these metrics are fairly good proxies of the distinct effects of vegetation complexity we sought to capture.

For arthropod data, we pooled abundance, richness, and predation data across all sites and sampling rounds. We kept arthropod data from visual surveys and pitfall traps separate since they represent foliage-level and ground-level foragers respectively. We used the log response ratio as our effect size for aphid and moth egg predation, calculated as LN(proportion prey removed in open treatments) - LN(proportion prey removed in bagged treatments). We conducted all analyses in R version 4.2.1 (R Development Core Team 2021).

We constructed four different groups of generalized linear models (GLMs) testing vegetation complexity metrics as predictors of the abundance and morphospecies richness of 1) herbivores, 2) natural enemies, 3) the two most abundant natural enemy taxa (ants and spiders), and 4) egg predation. For all model sets, we included vegetation density, diversity, and connectivity as predictor variables. For models of egg predation, we included natural enemy abundance and species richness as additional predictors. We used the variable inflation factor (VIF) to check for collinearity among these three variables using the ‘car’ package (Fox et al. 2007), and all VIF scores were under 2.4. We did not include site as a random effect because doing so resulted in overfitting. However, site did not have a significant effect on any predictor variable other than egg predation ($X^2 = 20.5$, df = 7, $p = 0.004$), and egg predation models with and without site as a random effect produced the same qualitative result. We tested all combinations of predictor variables and selected the top model based on AICc values. When the top model was within 2 AICc points of the next model, we averaged models using the ‘MuMIn’ package (Barton 2020). We used the ‘Dharma’ package in R to visually assess standard residual and QQ plots and determine the best error distribution for each response variable (Hartig 2021). We assumed a Poisson error distribution for herbivore richness, foliage-level natural enemy richness, ant richness, and spider richness models. We fit models of herbivore abundance, natural enemy abundance, ground-level natural enemy richness, ant abundance, and spider abundance with a negative binomial error distribution to account for overdispersion. For the effect size of egg predation (non-integer values), we used a gaussian error distribution.

Results

In total, we found 502 herbivores representing 11 families and 17 different morphospecies and 716 natural enemies from 23 families and 35 morphospecies (Table 1.2). The most common herbivore families were Aphididae (n = 323), Aleyrodidae (n = 113), and Cicadellidae (n = 38). Formicidae (n = 532) was the most abundant family of natural enemies, while the most speciose group of natural enemies was the order Araneae (n = 13).

Herbivorous arthropods did not show a significant response to any of the vegetation complexity factors considered here, while natural enemies consistently had positive associations with vegetation density in garden plots. Plots with high amounts of vegetation density supported more foliage-dwelling natural enemy morphospecies as well as a higher abundance of ground-dwelling natural enemies (Fig. 1.1a,b). The abundance of ground-dwelling natural enemies also had a negative association with vegetation diversity (Fig. 1.1c). Plots with high vegetation density had a higher abundance of spiders and more spider morphospecies (Fig. 1.1d-e), while ants did not respond to any vegetation complexity metric.

In aphid predation experiments, predators removed less than 10% of aphid prey, and there was no significant difference in the proportion of prey removed in open and bagged treatments (Fig. 1.2). For this reason, we did not conduct further analysis of aphid predation data. In contrast, about 40% of egg prey were removed in open egg predation treatments. The proportion of egg prey removed was about 4 times higher compared to bagged treatments (W = 2998.5, p = <0.001) (Fig. 1.2). None of the vegetation complexity factors we tested were significant predictors of egg predation, but we found that egg predation was positively associated with natural enemy abundance and negatively associated with natural enemy richness (Fig. 1.3).

Discussion

Overall, we found that of the three components of vegetation complexity examined (density, diversity, and connectivity), natural enemy abundance and richness responded to vegetation density and diversity, but herbivore abundance and richness and predation did not respond to any of the measured factors. Nevertheless, natural enemies removed up to 40% of egg prey in sentinel egg predation experiments, thereby providing important biological control services in gardens. However, while high natural enemy abundance increased egg predation, natural enemy richness resulted in a decline in egg predation, suggesting that antagonistic interactions between natural enemy species have negative impacts on egg predation.

First, the vegetation complexity factors we focused on had significant positive effects on natural enemies active on foliage. Gardener plots with a high density of vegetation supported more foliage-dwelling natural enemy morphospecies. In our study, vegetation density measures the percent cover of all vegetation, indicating the spatial extent of plants in a gardener plot. Plots with higher vegetation density thus provide more habitat structure and resources as well as shading that promotes cooler air temperatures and moisture retention (Avissar 1996, Gómez-Navarro et al. 2021). The importance of vegetation density in our system aligns with Mata et al. (2017), whose study of urban greenspaces in Australia showed strong positive responses of herbivores and predators to plant volume while responses to plant diversity were variable and species specific. Vegetation density in urban agriculture differs from vegetation density in rural agriculture, where monocultures of a single crop type make up most of the vegetation present in fields. Comparisons of monoculture and polyculture crop systems have largely found that natural enemies are more abundant in polyculture (Andow 1991, Letourneau et al. 2011), although experimental comparisons of monoculture and polyculture may confound plant diversity and plant density. One study examined variation in the size of Brassica plant species, which may be a better proxy for plant density, and found positive associations between plant size and natural enemy species richness (Schlinkert et al. 2015). In contrast, vegetation density in urban gardens includes a much larger diversity of crop plants (Thompson et al. 2003, Taylor et al. 2017), so garden vegetation density also contributes to habitat structural complexity. From this perspective, our results also agree with the findings of other studies of urban green spaces showing positive effects of vegetation structure and complexity on natural enemy abundance and species richness (Shrewsbury and Raupp 2006, Parsons and Frank 2019).

Further, plots with high vegetation density supported greater spider abundance and morphospecies richness on plot foliage, but vegetation complexity had no significant effect on ants. Spiders were the most diverse group of natural enemies in this study, and they include species with different foraging strategies such as web builders, wandering predators, and active hunters. For spiders, vegetation density may represent a greater availability of habitat and foraging locations as well as more prey. Previous studies support positive associations between spider abundance and richness and vegetation cover and structure in urban settings (Lowe et al. 2018, Delgado de la flor et al. 2020). With respect to ants, our study agrees with the findings of several other urban ant studies that have documented negative or no effects of vegetation structure on ant species richness (Lassau and Hochuli 2004, Clarke et al. 2008, Uno et al. 2010, Ossola et al. 2015). Vegetation structure effects on ants can depend on factors such as ant size and morphological traits. Since ants are highly active foragers, vegetation structure has implications for energy expenditure, with complex structured habitats being less energy efficient to navigate, especially for small ants (Lassau and Hochuli 2004). In contrast, large ant species can be more common in complex habitats with multiple layers of vegetation due to larger foraging areas (Nooten et al. 2019). While vegetation complexity supports a diversity of abundant garden spider species, it may not directly benefit the ant species found in our garden sites.

Vegetation complexity had variable impacts on ground-dwelling natural enemies. Vegetation density was positively associated with the abundance and diversity of ground-dwelling natural enemies, whereas vegetation diversity was negatively associated with the abundance of ground-dwelling natural enemies. The positive effects of vegetation density on natural enemies that forage at the ground-level indicates that ground arthropods may benefit indirectly from vegetation density. For instance, plots with more vegetation likely accumulate more leaf litter or correlate to other changes in ground cover and microclimate, which can influence ground arthropod community composition (Norton et al. 2014). A larger volume and depth of leaf litter provides important microhabitats and greater prey availability that can support ground foraging natural enemy species, such as spiders (Uetz 1979). Spiders made up about half the ground natural enemy species we sampled and may thus have a large influence on the positive effects of vegetation density we observed. On the other hand, ants were the most abundant ground natural enemy and had several non-significant negative associations with vegetation diversity, suggesting that ants may be driving the negative association between the abundance of ground natural enemies and vegetation diversity. Ants are generalist predators that can also form mutualistic associations with honeydew producing hemipterans that accumulate on plants (Detrain et al. 2010). All four ant species found in pitfall traps also occurred on plant foliage. Therefore, it is possible that ants spend more time foraging on foliage when more plant species are present in gardener plots due to greater availability of prey and mutualist species, resulting in a decline in ant abundance at the ground level. One previous study showed that Argentine ants were ten times more common on foliage when aphid mutualists were present compared to when aphids were absent (Grover et al. 2008). Greater plant diversity and associated herbivores may thus be shifting the foraging location of ants in our study.

In contrast, we did not find a significant effect of garden plot vegetation complexity on either herbivore abundance or morphospecies richness. This result is consistent with the findings of (Lowenstein and Minor 2018), who found no effect of garden characteristics on herbivore populations in residential gardens, community gardens, and urban farms. They propose low herbivore abundances as a possible explanation for this lack of effect. In our study, we found between 1 and 4 herbivore morphospecies and 1 to 108 herbivore individuals per plot, which is similar to the herbivore abundances reported by Lowenstein and Minor (2018). It is also possible that herbivores are responding to garden characteristics that we did not measure in this study. For instance, previous studies of this system have found that the number of *Brassica oleracea* plants across the whole community garden has positive effects on the density of aphids and other garden herbivores that feed on *B. oleracea* (Egerer et al. 2018a, Philpott et al. 2020b). The herbivores sampled in this study use a range of garden crops as host plants, and the abundance of their respective host plants may be an important factor in determining herbivore abundance and richness, especially for herbivores who specialize on particular host plants (Santolamazza-Carbone et al. 2014). Additionally, the effect of vegetation complexity is likely impacted by species traits such as diet breadth, mobility, and feeding mode (Moreira et al. 2016). Aphids and whiteflies, the two most common herbivore species in this study, differ in their mobility levels and dispersal modes. Non-winged aphids generally have low mobility, and winged, dispersing aphid morphs are weak fliers that are largely carried by wind patterns and may thus face challenges in navigating fragmented, heterogenous landscapes (Kring 1972). On the other hand, whitefly adults are stronger fliers capable of dispersing over 5 km and less dependent on wind for dispersal (Byrne 1999). Similar differences in mobility can alter herbivore responses to vegetation heterogeneity, with high mobility herbivore populations being less affected by the composition and fragmentation of vegetation patches compared to lower mobility herbivores (Banks 1998).

While our study did not detect a significant effect of any of vegetation complexity metrics on egg predation, natural enemy abundance was positively associated with egg predation. Natural enemies were active and removed up to 40% of prey from egg predation experiment plants within 24 hours. Natural enemies increased in abundance in response to vegetation density in gardener plots, suggesting that vegetation complexity indirectly supports biological control by supporting greater numbers of natural enemies. However, natural enemy species richness was negatively associated with egg predation. Based on the species composition of natural enemies present in gardens, one proposed explanation for this result is that intraguild predation among natural enemy species is limiting egg predation. For instance, spiders are generalist predators that often engage in intraguild predation of smaller spiders and other natural enemies (Hodge 1999, Saqib et al. 2021), which can have consequences for biological control. One study of biological control in grass-clover fields manipulated the number of wolf spiders in fields and observed no impact on prey taxa when the number of wolf spiders was increased (Birkhofer et al. 2008). However, fewer wolf spiders elevated the abundance of other ground spiders, suggesting that competition among spider species can interfere with biological pest control. Evidence from spider molecular gut content analysis shows that intraguild predation among spiders is more common when diverse prey are unavailable and resource niches are limited (Uiterwaal et al. 2023). Thus, low numbers of herbivores along with a diverse spider community could account for the negative impact of natural enemy richness on egg predation observed in our study.

Additionally, the presence of the Argentine ant, a species that is often aggressively invasive within its territory (Holway 1999), may also play a role in limiting biological pest control by other ant species. Previous work has documented that Argentine ants can reduce the foraging success of native ant species by outcompeting foraging native ants and successfully fighting off native ants from food baits (Human and Gordon 1996, Rowles and O'Dowd 2007). While we did not directly observe aggression between Argentine ants and other species, high Argentine ant abundance in our study suggests that antagonistic interactions occur and potentially reduce biological pest control. Our study represents a brief snapshot of the arthropod community in gardens, and longer-term study would be necessary to confirm whether antagonism between natural enemy species presents a cause for concern in the provision of biological control. Future research could clarify whether Argentine ants specifically hinder biological control in gardens.

Conclusion

This study shows that vegetation density is an important component of vegetation complexity in community gardens with implications for the natural enemy community supported by garden plots. Garden plots with higher vegetation density boosted the overall species richness of foliage-dwelling natural enemies and the overall abundance of ground-dwelling natural enemies. Additionally, spiders were more abundant and speciose in plots with high vegetation density. We also found a negative association between vegetation diversity and the abundance of ground-dwelling arthropods, but this result is likely driven by a shift in ant foraging activity from the ground-level to plot foliage when vegetation diversity is high. Our results generally support the idea that structurally complex vegetation supports natural enemy diversity and abundance, as predicted by the enemies hypothesis. In community gardens where vegetation diversity is inherently high due to the diversity of gardeners and growing practices, vegetation density may be relatively more important to manage as a component of habitat complexity.

Despite the increases in natural enemy abundance and diversity documented in our study, the herbivore community and egg predation were unaffected by vegetation complexity, possibly due to antagonistic interactions between natural enemy species. Our study suggests that antagonism between natural enemy species may potentially limit the provision of biological control by natural enemies engaged in intraguild predation or interference competition. If severe antagonism persists, future research could determine ecological conditions that result in natural enemy antagonism and possible mitigating factors. However, conserving natural enemies in garden plots arguably benefits the entire community garden, and our study supports the idea that abundant natural enemies can enhance pest suppression in garden plots. Overall, our results demonstrate that the decisions gardeners make about the vegetation in their garden plots have consequences for the natural enemies inhabiting community gardens. Based on these results, one management recommendation gardeners can implement is to add more vegetation cover in their plots to increase structural complexity and promote recruitment of natural enemies.

Author's contributions

AL led study design, fieldwork, lab work, data analysis, and prepared a draft of the manuscript. SMP contributed to field research design and logistics, data analysis, and manuscript editing.

Funding

This study was funded by the Heller Agroecology Graduate Student Research Grant. Additional support was provided by USDA-NIFA grant 2016-67019-25185 to SMP.

Table 1.1 Pearson correlation matrix of vegetation complexity variables (n = 64) in urban community garden plots in the California central coast.

	Density	**Diversity**	**Connectivity**
Density	-	0.55*	0.44*
Diversity	0.55*	-	0.10
Connectivity	0.44*	0.44	-

* $p < 0.05$

Table 1.2 Natural enemy and herbivore morphospecies observed in visual surveys and pitfall traps deployed in urban community gardens in the California central coast.

Trophic group	**Order**	**Family**	**Morphospecies**	**Visual survey count**	**Pitfall trap count**
Natural enemies	Araneae	Anyphaenidae	*Anyphaena sp. 1*	3	3
		Clubionidae	*Clubionidae sp. 1*	5	0
		Dysderidae	*Dysdera crocata*	0	4
		Gnaphosidae	*Scotophaeus blackwalli*	0	4
		Linyphiidae	*Erigone sp. 1*	3	0
			Lyniphiidae sp. 1	0	1
			Microlinyphia sp. 1	3	1
			Neriene dana	0	2
			Neriene digna	0	1
		Lycosidae	*Arctosa sp. 1*	0	10
			Pardosa sierra	2	0
			Pardosa sp. 1	1	7
		Salticidae	*Saliticae sp. 1*	2	0
		Tetragnathidae	*Tetragnatha sp. 1*	3	0
		Theridiidae	*Enoplognatha ovata*	1	0
			Latrodectus hesperus	2	0
			Neriene sp. 1	2	0
			Parasteatoda/Cryptachaea sp. 1	4	0
			Steatoda nobilis	2	0
			Steatoda sp. 1	2	0
			Theridion sp.1	1	0
		Zoropsidae	*Titiotus sp. 1*	0	2
			Titiotus sp. 2	0	1
	Carabidae	Carabidae	*Carabidae sp. 1*	0	2
			Laemustenus contemplanus	0	1
			Scaphinotus sp. 1	0	1
	Coleoptera	Staphylinidae	*Staphylinidae sp. 1*	2	25
			Sunius sp. 1	1	0
		Tenebrionidae	*Coelocnemis californica*	0	1
	Diptera	Dolichopodidae	*Dolichopidae sp. 1*	12	0
		Mecoptera	*Mecoptera sp. 1*	1	0
		Syrphidae	*Syrphidae sp. 1*	47	0
	Hemiptera	Anthocoridae	*Anthocoridae sp. 1*	1	0
		Geocoridae	*Geocoris sp. 1*	1	6
		Nabidae	*Nabis sp. 1*	1	1
	Hymenoptera	Formicidae	*Cardiocondyla mauritanica*	2	10
			Hypoponera opacior	1	6
			Linepithema humile	311	112
			Monomorium ergatogyna	34	53
			Prenolepis imparis	3	0
			Tetramorium sp. 1	1	0
		Mymaridae	*Mymaridae sp. 1*	1	0
		Platygastridae	*Platygastridae sp. 1*	1	0

	Opiliones		*Opiliones UnkGenSp*	6	0
			TOTAL	462	254
Herbivores	Coleoptera	Chrysomelidae	*Acalymma vittatum*	3	NA
			Chrysomelidae UnkGenSp	4	NA
			Diabrotica sp. 1	2	NA
			Epitrix hirtipennis	2	NA
		Ptinidae	*Stegobium paniceum*	1	NA
		Scraptidae	*Scraptidae UnkGenSp*	1	NA
	Diptera	Sciarcidae	*Sciarcidae UnkGenSp*	2	NA
	Hemiptera	Aleyrodidae	*Bemisia tabaci*	113	NA
		Aphididae	*Acyrthosiphon pisum*	94	NA
			Aphis fabae	154	NA
			Brevicoryne brassicae	72	NA
			Myzus persicae	1	NA
		Cicadellidae	*Empoasca sp. 1*	12	NA
			Euscelidius sp. 1	4	NA
		Miridae	*Miridae UnkGenSp*	20	NA
	Lepidoptera	Pieridae	*Pieris rapae*	14	NA
	Trombidiformes	Tetranychidae	*Tetrachynus sp. 1*	3	NA
			TOTAL	502	NA

Table 1.3 Model output from generalized linear models testing relationships between vegetation complexity metrics, herbivore and natural enemy variables, and egg predation in urban community gardens in the California central coast. Natural enemy sampling method is indicated by VS (visual survey) or PT (pitfall trap).

Response variable	**Model type**	**No. models**	**Predictor variables**	**No. models including variable**	**Estimate**	**z or t* value**	**p-value**
Herbivore abundance	Average	4	Density	1	-0.018	1.66	0.096
			Diversity	1	-0.091	1.36	0.173
			Connectivity	1	-11.3	0.929	0.353
Herbivore richness	Average	2	Density	1	0.005	0.932	0.351
VS Natural enemy abundance	Best	1	(Intercept)	NA	2.00	11.8	<0.001
PT Natural enemy abundance	Average	3	Density	2	0.02	2.032	**0.042**
			Diversity	1	-0.106	1.983	**0.047**
VS Natural enemy richness	Average	3	Density	3	0.013	2.59	**0.009**
			Diversity	2	-0.014	0.566	0.571
			Connectivity	1	-0.176	0.112	0.911
PT Natural enemy richness	Average	5	Density	2	0.009	1.14	0.255
			Diversity	2	-0.063	1.37	0.172
			Connectivity	1	4.16	0.734	0.463
VS Ant abundance	Average	2	Diversity	1	0.039	0.727	0.467
PT Ant abundance	Average	5	Density	2	0.021	1.87	0.062
			Diversity	2	-0.111	1.67	0.094
			Connectivity	1	8.01	0.909	0.363
VS Ant richness	Average	2	Density	2	0.009	1.28	0.201
			Diversity	1	-0.045	1.07	0.285
PT Ant richness	Average	3	Diversity	1	-0.042	1.07	0.286
			Connectivity	1	4.67	0.831	0.406
VS Spider abundance	Average	2	Density	2	0.01	2.02	**0.044**
			Diversity	1	-0.017	0.511	0.61
PT Spider abundance	Average	5	Density	3	0.033	1.78	0.075
			Diversity	1	-0.136	1.47	0.143
			Connectivity	2	15.6	1.19	0.232
VS Spider richness	Average	5	Density	2	0.022	2.34	**0.02**
			Connectivity	1	-5.06	0.616	0.538
PT Spider richness	Average	3	Density	2	0.023	1.65	0.099
			Diversity	1	-0.149	1.83	0.066
Egg predation	Average	4	Density	2	0.003	1.52	0.128
			Diversity	1	-0.009	0.855	0.393
			Natural enemy abundance	4	0.012	3.25	**0.001**
			Natural enemy richness	3	-0.084	2.1	**0.036**

* z-value for averaged models, t-value for best models

Figure 1.1 Relationships between significant vegetation complexity factors and the abundance and species richness of all natural enemies (a-c), spiders (d-e), and ants (f). Each dot represents a sampled plot at community garden sites in the California central coast. Lines show the fitted model and grey shading indicates model confidence bands (95% confidence interval).

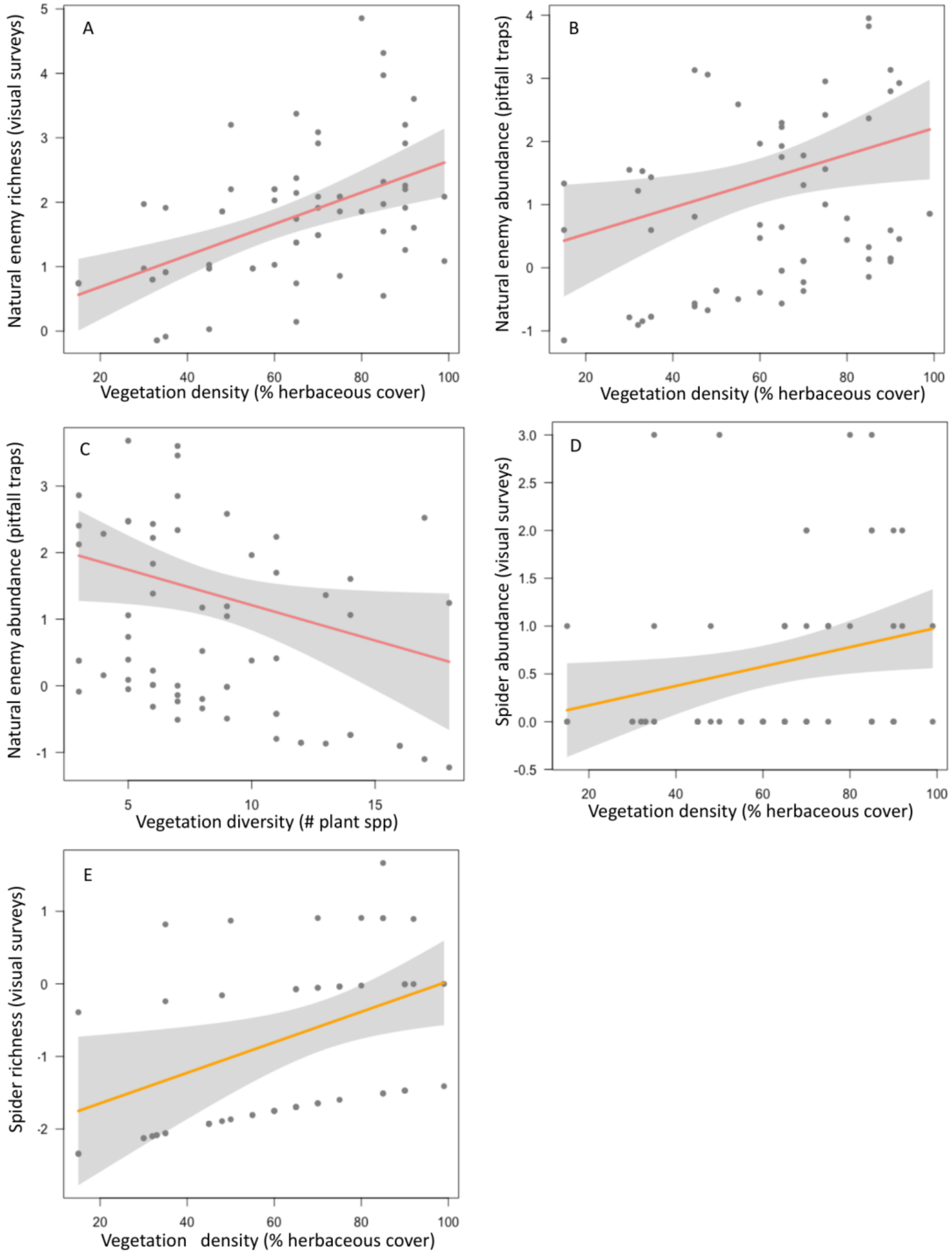


Figure 1.2 Results of sentinel pest predation experiments conducted in gardener plots at urban community gardens in the California central coast. Bars show proportions of prey removed (aphids, cornworm eggs) removed from open and bagged (natural enemy exclusion) fava bean plants after 24 hours. Error bars represent one standard error. The proportion of prey removed was significantly different between open and bagged treatments for eggs (W = 2998.5, p = <0.001) but not aphids.

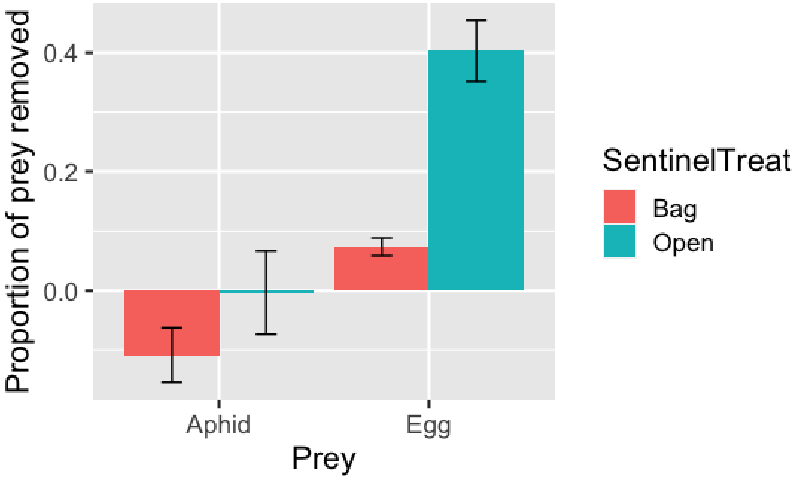
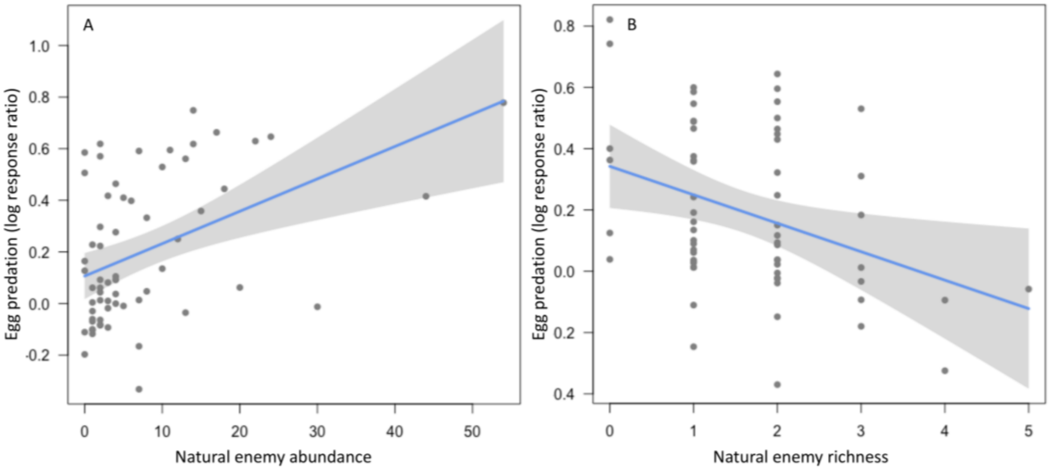


Figure 1.3 Relationships between significant predictors and egg predation in sentinel pest experiments at urban community gardens in the California central coast. Egg predation was positively associated with natural enemy abundance (A) and negatively associated with the species richness of natural enemies (B). Each dot represents a sampled plot at community garden sites in the California central coast. Lines show the fitted model and grey shading indicates model confidence bands (95% confidence interval).



CHAPTER 2: Shifts in host–parasitoid networks across agroecosystem management and urban landscape gradients

Abstract

Biological pest control relies on interactions between herbivores and their natural enemies. Maintaining this ecosystem service requires considering herbivore and natural enemy interactions and their response to anthropogenic change at multiple scales. In this study, we use ecological networks to quantify the network structure of interactions between herbivorous insects and their parasitoids. We examine how herbivore host abundance, parasitism rates, and shifts in network structure relate to changes in local habitat management and landscape context. We sampled herbivores and parasitoids in *Brassica oleracea* at 22 urban gardens in the California central coast. At each site, we measured local management characteristics (e.g. vegetation, ground cover, canopy cover), quantified surrounding landscape composition (e.g. urban, natural, open, and agricultural cover), and calculated three network structure metrics (interaction richness, vulnerability, and functional complementarity). We used generalized linear and mixed models to examine relationships between herbivore host abundance, parasitism rates, garden management and landscape characteristics, and network metrics. We found that both local management and landscape composition influenced herbivore host abundance and parasitism, while only local factors affected network structure. Higher network interaction richness was associated with enhanced parasitism rates for two host species and lower parasitism rates for one host species. Our results suggest that local garden management decisions can shift the

structure of host–parasitoid networks, which may subsequently affect host parasitism rates, but outcomes for biological pest control will likely vary across host species.

Introduction

Species interactions form the basis of ecological communities and are the foundation of many ecosystem services. In urban systems, anthropogenic transformation of land and resources drives habitat loss and fragmentation and decreases species richness and abundance (Alberti 2005, McKinney 2008). Yet, cities are heterogenous landscapes composed of a mosaic of land-use types, including intensive development and less intensive land-uses that preserve native habitats or produce novel habitats across the region (Lin and Fuller 2013). The different land-cover types (e.g. native, developed, or agricultural) in urban regions act as environmental filters that determine community composition (McIntyre et al. 2001). For instance, the composition and connectivity of the landscape influences dispersal and community assembly depending on species diet specialization and mobility (Burkman and Gardiner 2014, Egerer et al. 2017b, Liere et al. 2019). Further, local-scale human management of urban green spaces can make water, nutrient, and plant resources locally abundant, supporting higher trophic level species. As a result, complex networks of species interacting through herbivory, predation, parasitism, and competition persist (Alberti et al. 2003, Faeth et al. 2005). In particular, arthropods are abundant in urban systems and their interactions with other species contribute key ecosystem services such as pollination, decomposition, and biological pest control (Faeth et al. 2011, Lin et al. 2015). Maintaining these ecosystem services in urban systems thus requires understanding how human modification of urban habitats at multiple scales alters networks of species interactions.

Ecological networks depict pairwise species interactions as linear connections between nodes, providing a powerful tool that illuminates the underlying structure of community interactions and its responses to anthropogenic modification of landscapes (Tylianakis and Morris 2017). For example, in tropical, rural landscapes, agricultural intensification alters host–parasitoid interaction networks, resulting in low complexity (i.e. low numbers of links per species on average), uneven interaction strengths, and species homogenization (Tylianakis et al. 2007, Laliberté and Tylianakis 2010). The effect of urbanization on ecological networks is less well-documented, but evidence suggests fewer pollination interactions in urban sites compared to semi-natural and agricultural sites (Geslin et al. 2013) and fewer antagonistic interactions in urban sites surrounded by more agricultural land-use (Philpott et al. 2020b).

One challenge arising with the emergence of shifts in network structure is that the implications of network structure for ecosystem function and services remain variable and unclear. For one, the type of species interaction represented by the network can influence the ecological significance of network structure. A meta-analysis of 54 networks found that high network connectance (the proportion of realized links out of all possible links) promotes community stability in mutualistic networks composed of pollinators and plants whereas low network connectance promotes stability in antagonistic networks of herbivores and plants (Thebault and Fontaine 2010). These distinct associations between network structure and stability are likely due to prevailing community dynamics that vary between mutualistic and antagonistic networks. Positive indirect effects, such as facilitative interactions, are more common in mutualistic networks and can promote greater community robustness in strongly connected networks, while competitive interactions are more common in antagonistic networks and more weakly connected networks may therefore make them more robust (Thebault and Fontaine 2010, Bascompte and Jordano 2014).

Moreover, few studies have considered the effects of network structure on ecosystem function and services, and those that do report conflicting results (Tylianakis and Binzer 2014). In one plant–herbivore–parasitoid system, network structure differed between organic and conventional farms, but there were no differences in either parasitism or robustness to species loss (MacFadyen et al. 2009). On the other hand, a host–parasitoid–hyperparasitoid study found that organically managed fields in complex landscapes had simpler networks with fewer species and interaction links compared to conventionally managed fields in simplified landscapes, and that simple networks correlated with higher parasitism rates, lower pest abundances, and less incidence of hyperparasitism, an ecosystem disservice (Gagic et al. 2012). Evidently, the consequences of network structure vary with environmental and ecological community characteristics. This ecological context should be accounted for in order to decode network structure and apply insights to supporting interaction-based ecosystem functions and services.

Urban agroecosystems are ideal for investigating network structure, its implications for ecosystem services, and its response to gradients of local habitat management and urbanization in the landscape. Gardens provide habitat and resources that support urban biodiversity, including beneficial species that provide pest control (Lin et al. 2015) but also herbivorous species considered crop pests (Raupp et al. 2001). In fact, urban gardeners report facing significant challenges in managing pests on their crops (Oberholtzer et al. 2014). Natural enemies, such as predators and parasitoids, reduce herbivory damage and crop losses. Parasitoid wasps are particularly effective biological control agents (Schmidt et al. 2003), but their effectiveness can be moderated by the landscape context and local garden management practices. At the landscape scale, impervious surfaces in heavily urbanized landscapes can disrupt parasitoid habitat connectivity and host availability (Nelson and Forbes 2014), reduce parasitoid diversity (Bennett and Gratton 2012, Burks and Philpott 2016), and limit the ability of parasitoids to regulate herbivore populations (Kruess and Tscharntke 1994). Despite this limitation, the presence of large habitat patches connected by short distances in urban settings can support greater parasitoid species richness and higher rates of parasitism (Fenoglio et al. 2013). At the local scale, incorporating important parasitoid resources, such as flowers, may also help maintain diverse parasitoid populations in urban areas (Bennett and Gratton 2012). Considering both local and landscape processes may therefore be important for interpreting shifts in the network structure of urban agroecosystems and promoting interactions between parasitoids and their hosts.

In order to address the gap in the literature on the ecological significance of network structure for urban agroecosystems, we examined how local garden management and landscape context affects host–parasitoid networks and parasitism rates within urban agroecosystems. Few studies have examined ecological networks in urban settings (but see Geslin et al. 2013, Pereira-Peixoto et al. 2016, Philpott et al. 2020), and, to our knowledge, none have specifically considered networks of herbivore hosts and their parasitoids in urban agroecosystems together with their implications for biological pest control. Given the importance of ecological context for establishing links between network structure and ecosystem function and services, we asked: 1) How does local garden management influence host abundance and parasitism in urban community gardens, 2) How does landscape context influence host abundance and parasitism, 3) Do local garden management and landscape context impact garden host–parasitoid network structure, and 4) Do shifts in garden host–parasitoid network structure predict shifts in host parasitism?

Materials and Methods

Study system

We studied host–parasitoid networks and parasitism rates in *Brassica oleracea* at 22 community gardens in the California Central Coast (Monterey, Santa Cruz, and Santa Clara counties) (Fig. 1). *B. oleracea* is a popular garden crop reliably found in great abundance at our study sites. Garden sites range in size (444 m^2 - 15,525 m^2), age (2 - 50 years of cultivation), gardener demographics, garden management practices, and surrounding landscape context (Burks and Philpott 2016, Philpott and Bichier 2017, Egerer et al. 2017b, 2020a, Liere et al. 2020). All garden sites are organically managed and separated from each other by a distance of at least 2 km. The gardens are located in two California ecoregions, the Monterey Bay Plains and Terraces (n = 15) and the Bay Terraces/Lower Santa Clara Valley (n = 7). The Monterey Bay Plains and Terraces ecoregion is characterized by a cool, marine-influenced climate in which summer fog is common (Griffith et al. 2016). Dominant vegetation includes coast live oak and California oatgrass in the plains, coastal scrub and sage in the dunes, and artichokes, strawberry, and lettuce in cropland. In contrast, the Bay Terraces/Lower Santa Clara Valley ecoregion is a predominantly urban and residential area characterized by a hot and dry climate with scarce amounts of original vegetation remaining. Data collection for this study took place monthly over two summers of field work in 2017 (May through September) and 2018 (June and July).

Garden habitat and management characteristics

We sampled canopy cover, vegetation, and ground cover each month within a 20 x 20 m plot at the center of each garden. We used a concave spherical densitometer to measure percent canopy cover at the center of the 20 x 20 m plot and 10 m north, south, west, and east of the center. We measured the abundance and species richness of all trees and shrubs and trees and shrubs in flower, and we counted the number of *B. oleracea* plants in the 20 x 20 m plot. We sampled herbaceous vegetation and ground cover in eight randomized 1 x 1 m quadrats within the 20 x 20 m plot. We identified all herbaceous plants to morphospecies, counted the number of flowers and species in flower, and measured the height of the tallest vegetation. We also estimated the percent ground coverage of bare soil, grass, herbaceous plants, rocks, leaf litter, straw, and mulch/wood chips in each quadrat. We averaged values for vegetation data across all sample dates within a year and across both years. For herbaceous plant richness, we calculated cumulative richness across all plots for each year, and then averaged across both years.

Landscape context

To characterize the landscape surrounding gardens, we used ArcGIS spatial statistics tools and the 2016 National Land Cover Database (NCLD, 30 m resolution). We calculated percentages of land-cover types in 1 and 2 km buffers around gardens and designated four land-cover types: 1) natural, consisting of NLCD categories deciduous, evergreen forests, mixed forests, dwarf scrub, shrub/scrub, and grassland/herbaceous); 2) open, including lawn grass, park, and golf courses; 3) urban, comprising low, medium, and high intensity developed land; and 4) agriculture, including pasture/hay and cultivated crops. Other land cover types consisted of less than 5% of the surrounding landscape and were not included. Additionally, we used the ‘vegan’ package in R (Oksanen et al. 2020, R Core Team 2020) to calculate landscape diversity within 1 and 2 km of gardens using a modified Shannon-Wiener diversity index (H’) per (Bennett and Gratton 2012).

Herbivore host and parasitoid sampling

During our first field season (May through September 2017), we sampled cabbage aphids (*Brevicoryne brassicae*), by far the most abundant herbivore on *B. oleracea* at our garden sites, and their parasitoids. We conducted monthly surveys of 10 haphazardly selected *B. oleracea* plants at each garden. We visually inspected each plant, recorded the number of healthy and parasitized *B. brassicae* encountered, and collected all mummies (parasitized *B. brassicae*) in vials. We kept mummies in vials topped with cotton under laboratory conditions for two weeks to rear parasitoids. We preserved the eclosed adult parasitoids in ethanol.

For our second field season (June and July 2018), we excluded the hyperabundant *B. brassicae* from our monthly surveys and conducted targeted sampling of the next most common *B. oleracea* herbivores. We haphazardly selected 20 *B. oleracea* plants at each garden and visually inspected each plant for cabbage whites (*Pieres rapae*), diamondback moths (*Plutella xylostella*), beet armyworms (*Spodoptera exigua*), cabbage loopers (*Tricoplusia ni*), harlequin bugs (*Murgantia histrionica*), and whiteflies (*Aleyrodes proletella*). We counted the number of herbivore individuals on each plant, noted their life stage (e.g. eggs, nymphs, larvae, adults), and collected them in labeled vials. We reared herbivores in small plastic cups covered with fine mesh under laboratory conditions for three weeks. We monitored herbivores daily and fed them an artificial diet for lepidoptera consisting of mostly soy flour and wheat germ from Frontier Agricultural Sciences (Newark, DE). We recorded the number of herbivores that remained healthy, the number of herbivores that were parasitized, and the number of parasitoids that emerged from each herbivore. We preserved eclosed parasitoids in ethanol and referenced Naumann (1991), Goulet and Huber (1993), and online resources (BugGuide 2003, UC IPM 2018) to identify parasitoids to species and morphospecies.

Parasitism calculations

We calculated parasitism rates for host species that were widespread in our system, which we defined as present in at least half our sites. Because parasitoid species can target particular life stages, such as parasitoids that selectively attack eggs, larvae, or adults (Colazza et al. 2004, van Oudenhove et al. 2017), we differentiated between life stages of host species. The exception to this was *B. brassicae,* for which we could not reliably identify life stages in the field, but we assumed most individuals were adults. Three host species were common enough to warrant analysis: *A. proletella* nymphs (present at 11 sites), *B. brassicae* (present at all 22 sites), and *P. rapae* larvae (present at 19 sites). We calculated four different measures of parasitism for each host species: 1) presence or absence of parasitism per site, 2) proportion of sampled *B. oleracea* plants with parasitized hosts, 3) presence or absence of parasitism per host individual, and 4) proportion of parasitized hosts. These measures consider parasitism at multiple scales, reflecting parasitoid foraging decisions at the site, plant, and host levels and the impact of parasitism on the host population (Fenoglio et al. 2017). The presence of parasitism per site is a coarse measure indicating whether parasitoids have sufficiently colonized a given site and is likely informed by habitat quality, such as host density and floral resources, as well as the connectivity of the surrounding landscape (Kruess and Tscharntke 1994, Tentelier and Fauvergue 2007). The proportion of *B. oleracea* with parasitized herbivores measures an intermediate scale of parasitism at which visual and olfactory cues may be especially relevant. This intermediate measure also captures the prevalence of parasitism within a garden site, indicating how widespread biological control is amongst gardener plots within a garden. The presence of parasitized host individuals represents a finer-scale measure that may reflect parasitoid assessment of host suitability. Finally, the proportion of parasitized hosts captures the size of the host population, which can affect the probability that a host will be attacked due to parasitoids searching for local concentrations of their hosts (Murdoch and Stewart-Oaten 1989, Philpott et al. 2009).

Host–parasitoid network assembly and quantification

We constructed host–parasitoid network matrices for each garden site, pooling by site all herbivore and parasitoid species found in 2017 (*B. brassicae* and their parasitoids) and 2018 (all other herbivore hosts and their parasitoids). We used our observations of adult parasitoid emergence from herbivore hosts to determine the frequency of host–parasitoid interactions between species pairs at each site. We then used the 'bipartite' package in R to quantify network metrics (Dormann et al. 2008) for each garden network. We calculated three network metrics relevant to provisioning parasitism: interaction richness (with calculated values ranging from

0.87-1.84), vulnerability (1-3.86), and functional complementarity (2.83-15.5). Interaction richness is the number of unique interaction links in a network and is theorized to contribute to community redundancy and robustness (Tylianakis et al. 2010). Vulnerability indicates the average number of parasitoid species interacting with each host species and has been correlated with greater parasitoid attack rates (Bersier et al. 2002, Tylianakis et al. 2007). Functional complementarity measures the level of resource sharing among parasitoid species and can have implications for pest control (Blüthgen and Klein 2011, Poisot et al. 2013). Greater functional complementarity in host resource use is associated with higher parasitism rates in host–parasitoid food webs from temperate forests (Peralta et al. 2014).

Data analysis

We used generalized linear models (GLMs) and generalized linear mixed effect models (GLMMs) to examine relationships between host abundance, host parasitism, network metrics, and the local and landscape characteristics of garden sites. Due to the large number of environmental variables in our study, we conducted a selection process to identify non-correlated and non-collinear predictor variables. First, we grouped variables into biologically similar groups (e.g. vegetation, ground cover, or landscape variables) and used Pearson's correlations to identify correlated variables. From these correlated variables, we selected one variable per biological grouping, choosing the variable with the highest correlation coefficient relative to other variables in the group. We also selected variables that were not correlated with any other. In total, we selected ten possible predictor variables: ecoregion, garden size, number of trees and shrubs in flower, percent grass cover, percent straw cover, number of flower species, number of *B. oleracea* in 20 x 20 plot, host species abundance, urban land cover within 1 km of gardens, and agricultural land cover within 1 km of gardens. Percent land cover at the 1 and 2 km scales were correlated (with the lowest R^2 being 0.82), so we chose the 1 km scale because it captures the dispersal ranges of focal host species and the foraging ranges of the small to medium-bodied parasitoid species in our study (Bennett and Gratton 2012, Egerer et al. 2017b, Ludwig et al. 2018). We used natural-log and square-root operations to transform predictor variables that were not normally distributed. As an additional check against collinearity, we calculated a variance inflation factor (VIF) using the 'car' package (Fox et al. 2007). We removed variables with the highest VIF scores using a stepwise process until all variables received VIF scores under 3. To determine the best error distribution for each model, we compared residual deviance and df values and ran asymptotic chi-square tests for goodness of fit to choose the distribution that provided relatively equal residual and df values and nonsignificant chi-square values. We used the 'Dharma' package in R to plot QQ and standardized residuals which we used to visually assess model fits (Hartig 2021), and we visualized significant variables using the 'visreg' function. All data analyses were conducted in R version 3.6.3 (R Development Core Team 2021).

We created four different groups of models to answer our four research questions. The first model set examined whether any local garden management and landscape context variables drive host abundance. We created GLMs for each of the three most common host species (*A. proletella*, *B. brassicae*, and *P. rapae*) with host abundance as the response variable and the selected local habitat and landscape variables as predictors. We used local variable values from the year each host species was collected, 2017 values for *B. brassicae* and 2018 values for *A. proletella* and *P. rapae*. We fit all abundance models with a negative binomial error distribution to account for overdispersed data. We ran models with all possible combinations of predictor variables using the 'glmulti' function in the 'MuMin' package (Barton 2020) and selected the best model based on sample size corrected Akaike Information Criterion (AICc) values. For model sets where the next best models were within two AICc points of the best model, we ran averaged models using the 'model.avg' function in 'MuMin.'

The second set of models considered whether any local garden management and landscape context variables drive host parasitism. We created GLMMs using the 'lme4' package (Bates 2007) to model each parasitism measure for each of the three most common host species as the response variable. We used site as a random effect and local habitat and landscape variables as predictor variables. We fit these models with a binomial error distribution because we modeled parasitism as a two-vector response variable (parasitized individuals, healthy individuals) using the cbind function. We created separate models for each host species and parasitism measure.

The third set of models examined local and landscape variables as predictors of host–parasitoid network metrics (interaction richness, vulnerability, and functional complementarity). We used GLMs for each network metric modeled separately as response variables with local and landscape variables as predictors, and we used a gaussian error distribution to fit them. For these models, we averaged local variable values from 2017 and 2018 because garden networks included species collected in both years.

Finally, the fourth set of models assessed whether any network metrics drive host parasitism in our three most common herbivore species. We used GLMMs fit with a binomial error distribution for each host species, including the parasitism measures as the response variables, site as the random variable, and each network metric as the predictors.

Results

We sampled 60,245 herbivorous insects across all sampling periods, representing nine morphospecies and four life stages. The most abundant species were *B. brassicae* (n = 57,346, *A. proletella* (n = 1,312), *P. rapae* (n = 812), *M. histrionica* (n = 353), and *T. ni* (n = 330). From 1,995 hosts, we reared 612 parasitoids of 23 different morphospecies. Most parasitoids were Hymenoptera from six families: Aphelinidae (n=15), Braconidae (n=206), Figitidae (n = 100), Ichneumonidae (n = 15), Platygastridae (n = 158), Pteromalidae (n = 49), Hymenoptera sp. 1 (n = 1), Hymenoptera sp. 2 (n = 63). Additionally, three parasitoid morphospecies were dipterans in the family Tachinidae (n = 5).

Four host species were attacked by multiple parasitoid morphospecies while the other five host species were attacked by a single parasitoid morphospecies. *P. rapae* had the most diverse set of parasitoids with a total of seven parasitoid morphospecies emerging from this host. Six parasitoid morphospecies emerged from *B. brassicae*, five morphospecies from *A. proletella*, and three morphospecies from *P. xylostella*. A large majority of parasitoids attacked only a single host species. The exceptions were two parasitoid morphospecies, an ichneumonid wasp and a wasp in the genus *Trissolcus*, which attacked two host species each. Host parasitism ranged widely between species. The highest incidence of parasitism occurred in two Lepidopteran species, *P. xylostella* (4 of 10 hosts collected were parasitized) and *S. exigua* (3 of 6 hosts collected were parasitized). The lowest incidence occurred in the three most common species, *A. proletella* (45 of 1,088 hosts collected were parasitized), *B. brassicae* (1,856 of 57,346 hosts collected were parasitized), *and P. rapae* (13 of 146 hosts collected were parasitized).

We generated 21 garden networks (one site had no parasitoid species and thus produced no network) that varied in number of interacting host and parasitoid species. Host species numbers ranged from 1 to 5, with a median of 1 host per network. The number of parasitoid species in networks ranged from 1 to 7, with 3 parasitoid species per network being most common. Due to the small size of many garden networks, we were only able to calculate network metrics for 8 sites.

Host abundance in relation to garden local and landscape characteristics

Pieris rapae larvae abundance responded to one local variable. Gardens with more flower species were associated with marginally higher *P. rapae* larvae abundance (coefficient = 0.962, p = 0.0759; Fig. 2). The conditional model average included eight models with the number of *B. oleracea* as a predictor in one model, the number of flower species in two models, and percent urban cover within 1 km of gardens in three models (see Table 1 for full summary of all GLM and GLMM results). *A. proletella* nymph abundance and *B. brassicae* abundance were not significantly correlated with any predictor variables.

Host parasitism in relation to garden local and landscape characteristics

Using site-level parasitism (the presence of parasitized hosts per site), *A. proletella* parasitism was predicted by one local factor. The presence of parasitized *A. proletella* increased in gardens with a greater abundance of *A. proletella* nymphs (coefficient = 0.025, p = 0.024; Fig. 3). The best model predicting site-level *A. proletella* parasitism included the abundance of *A. proletella* nymphs and the intercept. *B. brassicae* and *P. rapae* site-level parasitism were not significantly correlated with any predictor variables.

Examining plant-level parasitism (the proportion of *B. oleracea* with parasitized hosts), *B. brassicae* parasitism was best predicted by two local factors and one landscape factor. The proportion of *B. oleracea* with parasitized *B. brassicae* was higher in gardens with greater *B. brassicae* abundance (coefficient = 0.288, p = 0.009; Fig. 3) and was marginally higher in gardens with a higher proportion of urban cover in the landscape (coefficient = 0.006, p = 0.064; Fig. 3), while the proportion of *B. oleracea* with parasitized *B. brassicae* was marginally lower in gardens covered with more grass (coefficient = -0.111, p = 0.095; Fig. 3). The conditional model averaged 64 models with percent grass cover, *B. brassicae* abundance, number of *B. oleracea*, number of flower species, number of trees and shrubs in flower, and percent urban cover within 1 km included as predictors. Plant-level *A. proletella* parasitism and *P. rapae* parasitism were not significantly correlated with any predictor variable.

For individual-level parasitism (presence of parasitism per host individual) and population-level parasitism (proportion of parasitized host species), parasitism measures across all three most common host species were not significantly correlated with any predictor variable.

Network metrics and garden local and landscape characteristics

Of the three network metrics we examined, only vulnerability (the average number of parasitoid species per host) showed significant correlations with predictor variables. The conditionally averaged model for network vulnerability integrated four models and included two local factors, percent grass cover and the number of *B. oleracea,* as predictors. Specifically, gardens with more grass cover had networks with higher vulnerability (z = 2.095, p = 0.036, Fig. 4) while gardens with more *B. oleracea* had networks with lower vulnerability (z = 2.061, p = 0.039; Fig. 4).

Host parasitism measures and network metrics

Interaction richness was the only network metric that significantly correlated with host parasitism measures. For *B. brassicae*, population-level parasitism (the proportion of parasitized *B. brassicae* hosts) was marginally higher in gardens with higher interaction richness (z = 1.711, p = 0.087; Fig. 5). For *P. rapae*, plant-level parasitism (the proportion of *B. oleracea* with parasitized *P. rapae*) was marginally higher in gardens with higher interaction richness (z = 1.877, p = 0.061; Fig. 5). In contrast, individual-level *A. proletella* parasitism (presence of parasitized *A. proletella*) was marginally lower in gardens with higher interaction richness (z = -1.750, p = 0.080; Fig. 5).

Discussion

In this study, four local factors and one landscape factor were important predictors of host abundance and parasitism measures, whereas two local factors predicted host–parasitoid network structure. Additionally, we found evidence that network structure, specifically interaction richness, may influence host parasitism.

Abundance of one host species life stage, *P. rapae* larvae, was marginally higher in gardens with more flower species (Fig. 2). This observation may reflect the reliance of adult *P. rapae* on floral resources which adults seek out using color cues to guide their foraging (Arikawa et al. 2021). Diverse flower assemblages in gardens are likely to include flower species with nectar that is especially suitable to *P. rapae* and support high *P. rapae* egg and larvae abundances (Zhao et al. 1992, Winkler et al. 2010). While we present evidence that local habitat factors like flower diversity attract herbivores, flowers are simultaneously important resources for parasitoids and other natural enemies, and likely present a net benefit to biological pest control (Lowenstein and Minor 2018).

Of the local scale factors associated with host parasitism, host abundance was the strongest predictor of enhanced parasitism for two host species. Greater *A. proletella* nymph abundances positively associated with site-level presence of parasitized *A. proletella* nymphs, and greater *B. brassicae* abundances associated with a higher proportion of *B. oleracea* plants with parasitized *B. brassicae* (Fig. 3). These findings suggest a positive density dependent effect on parasitism, characterized by greater parasitism levels when host density is high, at both the site-level and plant-level. At the site-level, positive density dependence may occur because of parasitoid foraging behaviors that select for sites where they are more likely to find adequate hosts and food resources. According to optimal foraging theory, parasitoids that aggregate in high density patches of their host can maximize oviposition, which increases parasitism (Cook and Hubbard 1977, Walde and Murdoch 1988). At the plant-level, parasitoids respond to herbivore-induced plant volatiles that plants release after damage from herbivory (Turlings et al. 1990). *B. oleracea* release more volatile organic compounds when more herbivores are present, providing chemical cues that convey information about the location and density of hosts which parasitoids can use to inform host-searching decisions (Girling et al. 2011). Parasitoids can discriminate between volatile cocktails produced by plants with high and low host densities and show preferences for volatile cues from plants with high host densities (Geervliet et al. 1998, Girling et al. 2011).

In addition to host abundance, percent grass cover within gardens had a marginally negative correlation with the proportion of *B. oleracea* with parasitized *B. brassicae* (Fig. 3). At our garden sites, grasses grow in and around garden plots as weeds, or non-crop species, and are not planted intentionally as lawn cover. Grass cover also correlated positively with leaf litter cover ($R^2 = 0.69$), so more grass may indicate greater structural complexity in gardens. Habitat complexity includes diverse and heterogenous vegetation and ground cover, and complex-structured habitats have been associated with greater abundances of natural enemies, including parasitoids (Langellotto and Denno 2004). However, several lab and field studies examining the structural complexity of individual plants and the surrounding plant community have found that complex structures can disrupt parasitoid host-finding and reduce parasitism (Andow and Prokrym 1990, Gingras et al. 2003, Meiners and Obermaier 2004, Obermaier et al. 2008, Randlkofer et al. 2010a). This disruptive effect can arise when plant structural complexity provides physical refuges for herbivores to escape from natural enemies by making herbivores inaccessible or lowering the probability of their encounter (Price et al. 1980, Randlkofer et al. 2010a). High structural complexity may also alter plant volatile composition by introducing non-host specific volatiles and changing microclimatic conditions that affect the transmission of plant volatiles, potentially interfering with the ability of parasitoids to use volatile cues to locate prey (Randlkofer et al. 2010b). In our study, gardens with more grass cover may similarly disrupt parasitoid host-finding, although the mechanism is not certain.

At the landscape scale, urban cover within 1 km of gardens had a marginally positive correlation with the proportion of *B. oleracea* with parasitized *B. brassicae* (Fig. 3). In our study, *B. brassicae* was the most abundant host (n = 57,346) and parasitized *B. brassicae* occurred at each of our garden sites. Beyond measuring the presence of parasitism at a site, the proportion of *B. oleracea* with parasitized hosts indicates the prevalence of parasitism within a site. Our result suggests that *B. brassicae* parasitism is more widespread amongst *B. oleracea* plants within gardens surrounded by landscapes with more urban cover, potentially benefiting more gardeners. While parasitoid species richness generally decreases in more urban landscapes (Bennett and Gratton 2012, Burks and Philpott 2016), we previously found higher parasitoid abundances in gardens surrounded by more urban cover (Burks and Philpott 2016). Additionally, recent data from our system shows that urban land cover has much higher floral abundance compared to other land cover types (Philpott, S., unpublished data). Therefore, it is possible that the parasitoid species that attack *B. brassicae* locally concentrate in gardens embedded in highly urbanized, simple landscapes due to a relatively high availability of floral resources compared to the surrounding landscape (Tscharntke et al. 2012), and the local concentration results in higher parasitism.

Two local factors predicted network vulnerability, defined as the average number of parasitoids per host in the network. Gardens with more *B. oleracea* had lower network vulnerability, while gardens with more grass cover had higher network vulnerability (Fig. 4). High network vulnerability indicates a greater diversity of parasitoid species controlling each host species and has been associated with greater levels of parasitism through functional redundancy (Tylianakis et al. 2007). More *B. oleracea* per garden in our sites was previously associated with more herbivore species (Philpott et al. 2020b), which could reduce the ratio of parasitoids per host species and lower network vulnerability in gardens with high densities of *B. oleracea*. In contrast, gardens with more grass cover, or structural complexity, appear to support high network vulnerability. Our results therefore suggest that garden management that avoids high densities of *B. oleracea* crops and integrates structural complexity components like grass could boost vulnerability in host–parasitoid networks and potentially enhance herbivore parasitism in urban gardens.

However, network vulnerability can have variable outcomes for herbivore parasitism. Despite finding a positive effect of grass cover on network vulnerability (Fig. 4), gardens with more grass cover had lower plant-level *B. brassicae* parasitism (proportions of *B. oleracea* with *B. brassicae* parasitism; Fig. 3). Thus, high network vulnerability, or more parasitoid species per herbivore species, may not generate higher parasitism for every host species. In some systems, parasitoid diversity results in higher parasitism (Tylianakis et al. 2006, Fenoglio et al. 2013), but this is not true for every system (Menalled et al. 1999, Rodríguez and Hawkins 2000). The trophic effects of multiple predators can vary with the functional traits of the predator species (e.g. predator hunting mode and domain), the prey species (e.g. prey morphology and behavior), and the spatial environment they inhabit (Finke and Denno 2002, Wilby et al. 2005, Schmitz 2007). Parasitoid species assemblages with complementary foraging strategies, for example, species that attack hosts at different life stages or find host more efficiently on different crop varieties, can produce higher total parasitism rates (Macfadyen et al. 2011). For instance, Peralta et al. 2014 found that networks with higher functional complementarity led to higher parasitism even after accounting for differences in host and parasitoid richness. The effect of network vulnerability and other network metrics may thus be moderated by parasitoid and host species traits.

Garden networks with high interaction richness were associated with marginally higher parasitism for two host species, *B. brassicae* and *P. rapae*, and marginally lower parasitism for one host species, *A. proletella* (Fig. 5). Greater interaction richness denotes more interactions in the network overall and can generally support greater provision of ecosystem services and stability through ecological redundancy (Dyer et al. 2010, Tylianakis et al. 2010). The differential effects of interaction richness on parasitism across host species that we document here are likely informed by the identity of the parasitoid and host species and their intraguild interactions, which are not captured by bipartite networks. For example, in a predator–pathogen–prey system, antagonistic interactions between the predator and the pathogen control agents resulted in improved biological pest control, but only when the predator was the dominant control agent (Ong and Vandermeer 2014). In addition to absolute effects on parasitism, the functional redundancy provided by high interaction richness may help stabilize the variability of parasitism in some systems (Peralta et al. 2014). One caveat to our findings about interaction richness is that several garden networks were too small to quantify, which limited our sample size to eight garden sites. Despite this limitation, interaction richness consistently showed up as a predictor of parasitism across the three host species we examined, suggesting that this network metric in particular warrants further investigation.

Conclusion

Our study shows that characteristics of the local habitat and the landscape surroundings of urban gardens inform host abundance and parasitism while only the local habitat affects network structure. We document positive host density effects on parasitism in urban garden networks with a high degree of parasitoid specialism. We also show that gardens in heavily urbanized landscapes can still support high parasitism for certain host species. Our study indicates that structural complexity in the form of weedy grass cover within gardens can support high network vulnerability, a network structure thought to promote parasitism, but this may not translate to higher parasitism for every host species. Additionally, our study shows that the richness of interactions in a network can differentially influence parasitism across host species. While our study suggests relationships between garden local and landscapes factors, host–parasitoid interactions, and outcomes for biological pest control, further research, including field experiments, is necessary to explore the mechanisms driving these relationships. Biological pest control is often context-dependent, and that context extends to the traits and intraguild interactions of herbivore and natural enemy species. Future ecological network research could thus incorporate analyses of species traits and behaviors to shed light on ecological community factors that are not captured by bipartite networks alone but nonetheless have implications for species interactions and ecosystem service provision. However, extensive sampling may be required to assure adequate replication and greater analytical power.

Authors' contributions

AL and SMP contributed to research design. SMP acquired funding and led fieldwork and labwork logistics. AL, HL, and NS processed laboratory samples. AL completed data analysis and wrote the manuscript draft. All authors contributed to manuscript edits.

Funding

This work was financially supported by the Sustainable Agroecosystems: Health, Functions, Processes, and Management Program [grant no. 2016-67019-25185 / project accession no. 1009123], the Research and Extension Experiences for Undergraduates Program [grant no. 2016-67032-24987 / project accession no. 1009021] from the USDA National Institute of Food and Agriculture, the Ford Foundation's Predoctoral Fellowship program, the UC LEADS Program, and the University of California, Santa Cruz general funds.

Table 2.1 GLM and GLMM results examining relationships between host abundance, host parasitism, local habitat variables, landscape variables, and network metrics.

Response variable and predictors in averaged model	No. of models predictor was included in	Coefficient estimate	z or t value	p-value
P. rapae abundance				
No. flower species	2	0.962	1.775	0.076
No. *B. oleracea* 20 m*	1	-0.730	1.235	0.217
Urban 1 km	3	-0.013	0.918	0.359
A. proletella parasitism (site-level)				
A. proletella nymph abundance*	1	0.025	2.258	0.024
A. proletella parasitism (individual-level)				
Interaction richness	1	-3.917	-1.750	0.080
B. brassicae parasitism (plant-level)				
No. flower species	4	-0.298	1.494	0.135
B. brassicae abundance*	2	0.288	2.622	0.009
Urban 1 km	6	0.006	1.852	0.064
Grass 1 m	1	-0.111	1.671	0.095
No. trees and shrubs in flower	5	-0.009	0.334	0.739
No. *B. oleracea* 20 m*	3	0.014	0.126	0.900
B. brassicae parasitism (population-level)				
Interaction richness	1	0.522	1.665	0.096
Vulnerability				
Grass 1 m	1	0.115	2.095	0.036
No. *B. oleracea* 20 m*	2	-1.054	2.061	0.039
P. rapae parasitism (plant-level)				
Interaction richness	1	2.834	1.877	0.061

Note: Site-level parasitism indicates the presence of parasitized hosts per site. Plant-level parasitism is the proportion of sampled *B. oleracea* with parasitized hosts. Individual-level parasitism is the presence of parasitism per host individual. Population-level parasitism represents the number of parasitized hosts/total number of hosts. z-values are listed for averaged models and t-values for best models.

* ln-transformed variables

Figure 2.1 Map of the California central coast depicting garden sites and land cover types in the region of study.

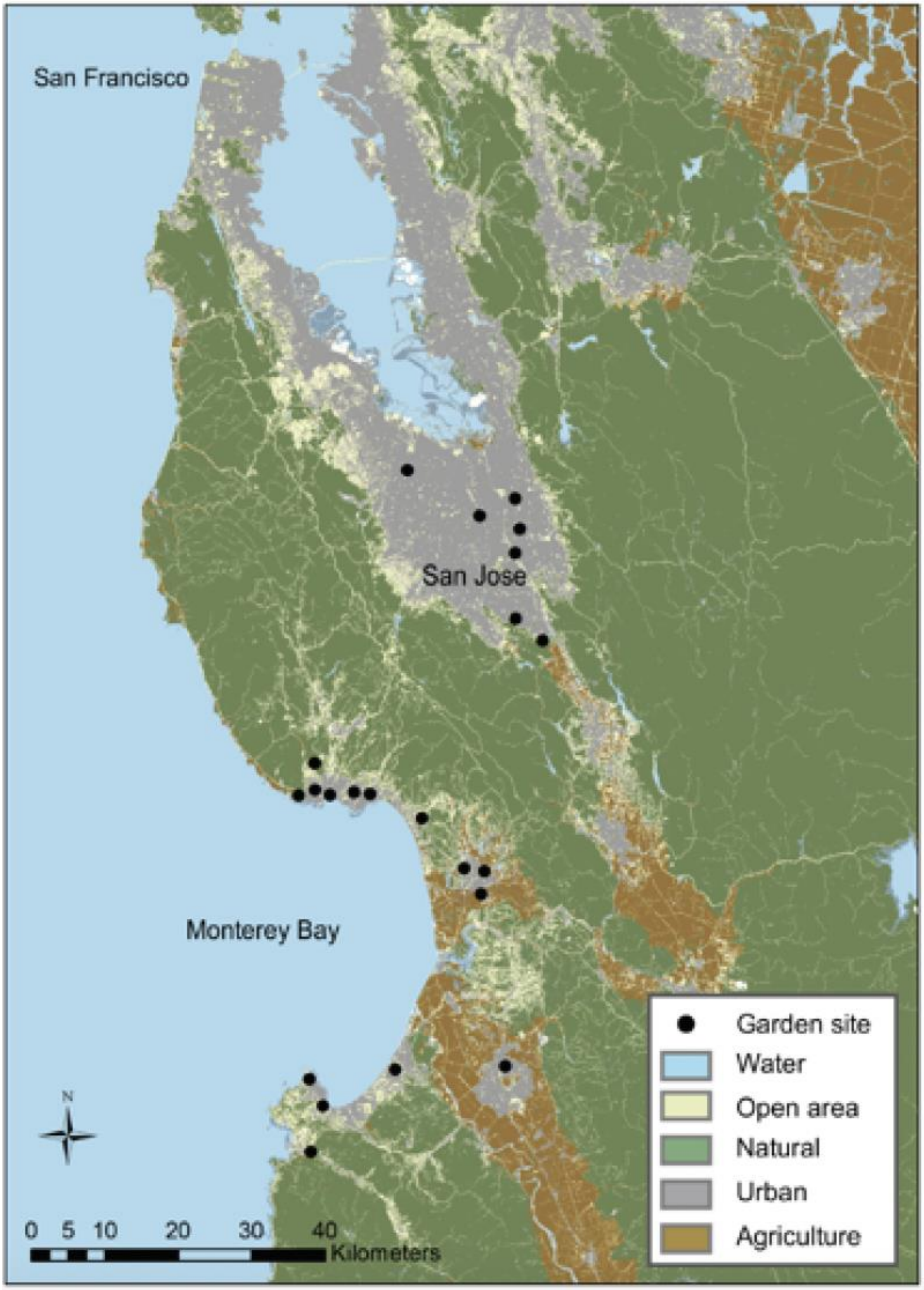


Figure 2.2 The positive response of *Pieres rapae* (cabbage white) larvae abundance to a local variable, the number of flower species in urban gardens in the California central coast (z = 1.775, p = 0.076). Line shows the fitted model and grey shading indicates model confidence bands (95% confidence interval).

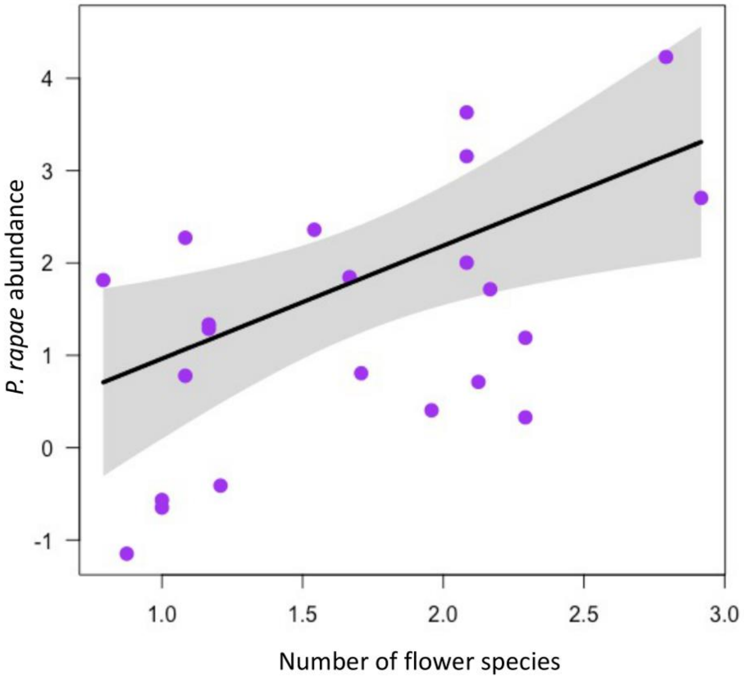


Figure 2.3 Host parasitism in response to three local factors and one landscape factor in urban gardens in the California central coast. (A) Site-level *Aleyrodes proletella* (whitefly) nymph parasitism shows a positive response to the abundance of *A. proletella* nymphs (z = 2.258, p = 0.024). (B) *Brevicoryne brassicae* (cabbage aphid) abundance (z = 2.622, p = 0.009) and (D) urban cover within 1 km of gardens (z = 1.852, p = 0.064) have a positive effect on plant-level *B. brassicae* parasitism. (C) Percent grass cover in gardens has a negative effect on plant-level *B. brassicae* parasitism (z = 1.671, p = 0.095). Lines show the fitted model and grey shading indicates model confidence bands (95% confidence interval).

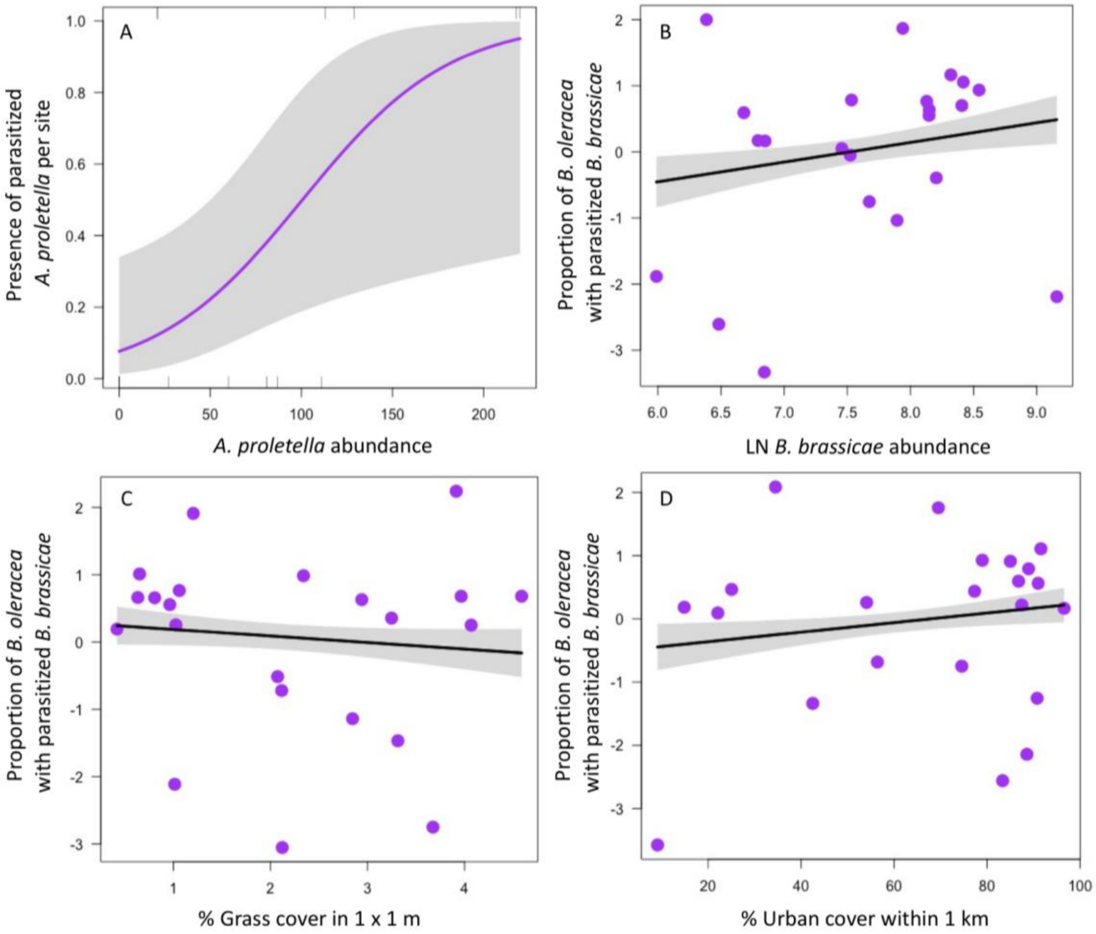


Figure 2.4 Network vulnerability in response to two local factors in urban gardens in the California central coast. (A) Vulnerability shows a positive response to percent grass cover (z = 2.095, p = 0.036). (B) The number of *Brassica oleracea* in gardens has a negative effect on vulnerability (z = 2.061, p = 0.039).

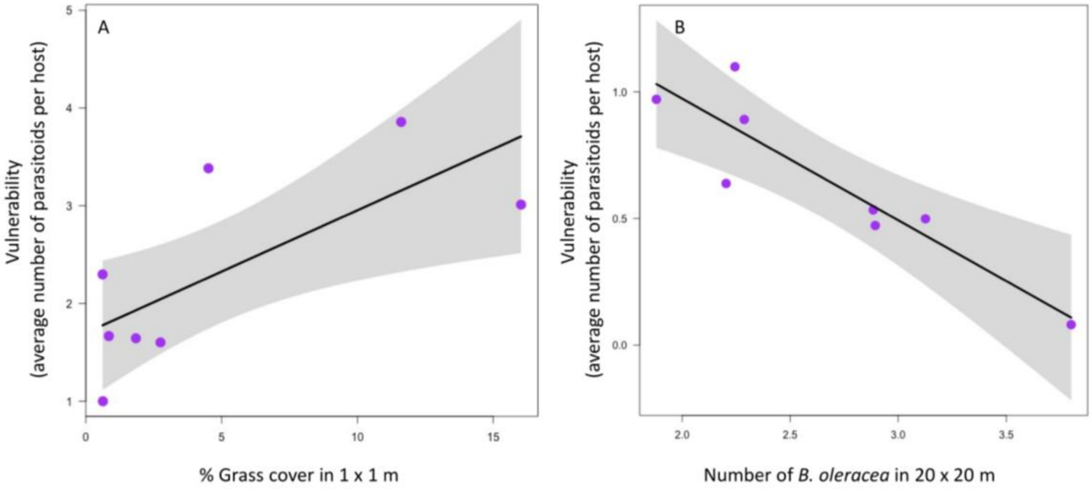
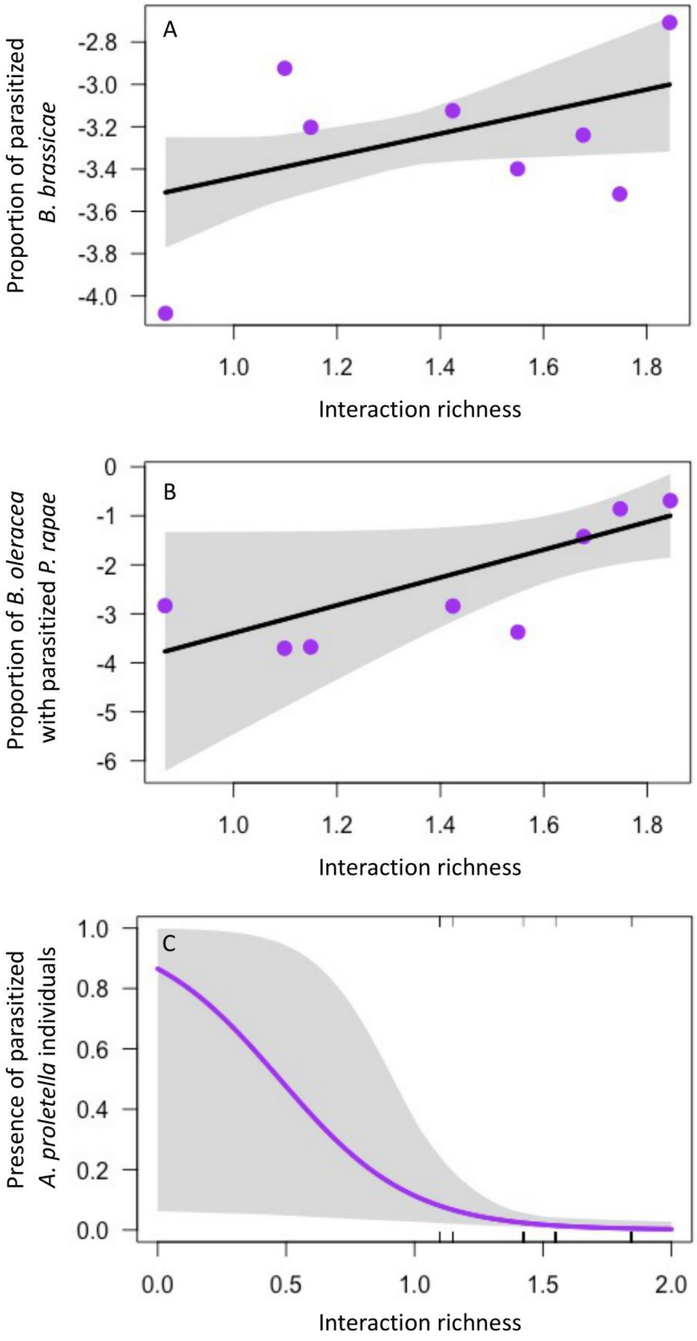


Figure 2.5 Associations between network interaction richness and host parasitism in urban gardens in the California central coast. (A) Population-level *Brevicoryne brassicae* (cabbage aphid) parasitism (z = 1.665, p = 0.0959) and (B) plant-level *Pieres rapae* (cabbage white) larvae parasitism (z = 1.877, p = 0.061) shows a positive response to network interaction richness. (C) Individual-level *Aleyrodes proletella* (whitefly) nymph parasitism shows a negative response to network interaction richness (z = -1.750, p = 0.080).



CHAPTER 3: Herbivore and natural enemy metacommunity structure in urban agroecosystems

Abstract

Urban green spaces, such as urban gardens, are distributed as patches of habitat capable of supporting high levels of biodiversity within a larger mosaic of urban landscape. Arthropods dispersing between urban gardens thus represent metacommunities of interacting species, including herbivore pests and their natural enemies. The metacommunity dynamics of these arthropods thus have consequences for the long-term persistence of natural enemies and biological pest control in urban agriculture. This study takes a pattern-based approach to investigate the metacommunity structure of herbivore and natural enemy communities in 24 community garden sites in the California central coast. We use the elements of metacommunity structure framework paired with a canonical correspondence analysis to determine the pattern that best describes the structure of arthropod metacommunities and assess garden habitat (e.g. garden size, vegetation cover, ground cover) and landscape characteristics (e.g. percent urban cover, landscape diversity) as drivers of metacommunity structure. We found that the herbivore metacommunity is best described by a Clementsian pattern while the natural enemy metacommunity follows a quasi-nested pattern, indicating that the metacommunity structure of both trophic groups is non-random and that species distributions are determined by a common environmental gradient. Landscape diversity corresponded

highly with the metacommunity structure of herbivores and ants. In contrast, a local garden habitat characteristic, the number of tree and shrub species in flower in gardens, was most highly associated with the metacommunity structure of all natural enemies as well as spiders. These results suggest that the composition of the urban landscape has a stronger impact on herbivore metacommunity structure, while the resources provided by urban garden habitats determine natural enemy metacommunity structure. Thus, by adding resources important for natural enemies, like flowering trees and shrubs, gardeners may be able to support metacommunities of natural enemies in this region.

Introduction

Urban arthropods navigate complex landscape mosaics shaped by patterns of human land use. Urban development transforms landscapes by fragmenting natural habitats, introducing impervious surfaces, and increasing pollution with negative impacts on urban biodiversity (McIntyre 2000, McKinney 2008, Faeth et al. 2011, Fenoglio et al. 2020). However, cities are also comprised of urban greenspaces, such as parks, gardens, and other low-intensity developments that preserve or add vegetation, providing habitat and resources that support urban species (Aronson et al. 2017). The resulting mix of both developed and greenspaces within urban areas means that urban species experience cities as fragmented patches of habitat (e.g. greenspace) embedded in an inhospitable matrix of impervious surfaces (e.g. developed areas) connected by the dispersal of organisms between patches. Compact or sprawling forms of urban development can influence the size of habitat patches as well as the degree of connectivity between patches (Lin and Fuller 2013). The effects of urban fragmentation on urban populations can depend on species-specific characteristics such as body size and dispersal ability (Keitt et al. 1997, Ong et al. 2020). For example, large or winged organisms with a high capacity for dispersal may perceive a highly fragmented habitat as a single patch, whereas smaller, less mobile species are less likely to disperse across fragmented habitat.

The patchiness of urban landscapes lends itself well to application of ecological theories of island biogeography and metapopulations, which consider the spatial context of habitats and their implications for species dispersal and ensuing population dynamics throughout landscapes (Niemelä 1999, Fattorini et al. 2018). Under a metapopulation framework, local patches of extinction-prone populations are connected through migration, allowing for regional persistence across a landscape (Levins 1969, Hanski 1998). Extensions of basic metapopulation theory include consideration of multiple interacting species, which are referred to as metacommunities. Metacommunity theory is based on the recognition that ecological communities often operate beyond a single habitat patch and are shaped by a combination of local and regional processes, as elucidated by the major theoretical paradigms that guide metacommunity research (Leibold et al., 2004). Under the patch-dynamic paradigm, species interactions occur across multiple, homogenous local habitats and can affect population migration and extinction rates at larger scales than a single local habitat. Regional coexistence of species in the metacommunity, such as predator and prey species, is often made possible by tradeoffs in competition and colonization abilities. In contrast, the species-sorting paradigm emphasizes heterogeneity in habitat patches based on differences in abiotic factors, such as soil type and resource availability. Differences in species requirements and preferences for specific local conditions results in local community composition that varies with environmental gradients, with local patches dominated by highly adapted species, allowing for regional coexistence of a high diversity of species (Suzuki and Economo 2021). In this case, environmental filtering is a key process that determines the distribution of species across the metacommunity region (Chase et al. 2020). When regional dispersal is very high, mass-effects can come into play. Under the mass-effects paradigm, local and regional population dynamics are quantitatively affected by dispersal. High dispersal into and out of patches can result in source-sink dynamics, whereby immigration rates enhance population growth in high quality patches and emigration out of low quality patches suppresses population growth (Amarasekare and Nisbet 2001). When dispersal is high and regional competition is strong, competitive exclusion at local patches across the region can also lead to lower overall diversity in the metacommunity (Suzuki and Economo 2021).

Understanding the interplay of local habitat characteristics and landscape context is critical for informing management of urban species, especially those involved in generating ecosystem services. Urban agroecosystems, such as urban farms and gardens, provide unique opportunities to investigate the interacting effects of urban landscape patterns and local habitat patch characteristics on regional arthropod metacommunities. Urban gardens often include high amounts of crops and ornamental plant species that support associated communities of herbivores, pollinators, and natural enemies (Lin et al. 2015), suggesting that urban gardens can function as patches of high-quality habitat in urban landscapes. However, the quality of garden habitat patches can be moderated by the availability of other suitable habitats in the urban landscape. For instance, a study comparing lady beetles in urban gardens in Michigan and California found that urbanization (measured as % impervious cover) had a negative effect on lady beetle abundance and diversity in Michigan but a positive effect on lady beetle abundance and diversity in California (Egerer et al. 2018c). The authors suggest that the relative abundance of verdant habitats surrounding gardens in Michigan may lead to gardens functioning as sink habitats, where populations decline without migration from other habitats. In contrast, drought conditions in California may increase the importance of irrigated garden habitats, which act as source-habitats capable of supporting positive population growth. Further, urban systems highlight the influence of the matrix on organism dispersal between focal patches of habitat. The intensity of urban development can moderate the permeability of the urban landscape for dispersing arthropods. While metacommunity models often assume that the matrix surrounding habitat patches is homogeneously unsuitable for organisms, in terrestrial systems matrix quality can vary from completely uninhabitable to suitable as habitat. A higher quality matrix allows for higher rates of migration, which in turn can facilitate the persistence of species in lower quality patches throughout a region (Vandermeer and Carvajal

2001). Species that are habitat specialists may also be less tolerant of a low quality matrix whereas habitat generalists are more likely to be able to survive in the matrix for some time as they disperse (Burkman and Gardiner 2014). Thus, the quality of both habitat patches and the urban matrix can inform the migration and diversity of arthropods in urban agroecosystems.

Researching how assemblages of natural enemies and their prey collectively respond to fragmentation is important for urban agriculture because metacommunity dynamics have implications for the long-term persistence of natural enemies and their provision of biological pest control. For instance, a study of spruce budworm parasitoids found that parasitoid metacommunity structure (i.e. diversity and abundance across sites) was largely shaped by the composition and configuration of tree cover in forests rather than herbivore densities (Marrec et al. 2018). In this case, altering landscape structure had the potential to introduce parasitoid dispersal limitations and could thus have significant impacts on herbivore outbreaks. Landscape-induced changes in herbivore migration may also have consequences for pest control. In a mesocosm study of an arthropod metacommunity in tropical terrestrial leaf litter, higher migration rates of non-predator arthropods resulted in higher extinction rates and lower species richness of predator arthropods (Hajian-Forooshani et al. 2019). Over time, lower predator species richness may likely result in less predation.

Of the few studies that have examined natural enemy metacommunities in urban landscapes, previous work indicates that the unique life history characteristics and morphology of different natural enemy taxa can lead to distinct responses to urban landscapes. In Paris, France, colonization of urban gardens by carabid beetles, which are largely unable to fly, was negatively affected by distance from source woodland habitats (Vergnes et al. 2012). In contrast, spiders were equally abundant in source habitats and urban gardens due to their higher capacity to disperse via ballooning behaviors. In Ann Arbor, MI, a study of a metacommunity of aphids, lady beetles, and parasitoid wasps in urban gardens found that lady beetles were affected only by local habitat quality while parasitoid wasps were affected by both local and landscape quality (Ong et al. 2020). The authors suggest that lady beetles may face greater dispersal limitations in urban landscapes compared to more agile parasitoids. Thus, both species traits and the spatial context of the landscape can determine metacommunity patterns and outcomes for pest control.

Metacommunity theory takes two main approaches to investigating metacommunities—a mechanism-based approach and a pattern-based approach (Mihaljevic 2012). The mechanism-based approach explicitly considers the effects of dispersal, migration, and extinction rates in determining metacommunity dynamics (Cottenie 2005). In contrast, the pattern-based approach examines metacommunity structure, as defined by species-by-site matrices of presence and absence, in order to infer possible community assembly mechanisms and evaluate their relative influence (Presley et al. 2010). Empirical measurement of dispersal patterns remains a challenging effort, in particular for small organisms such as urban arthropods which can be difficult to mark and successfully recapture (Nathan 2001). While technological advancements have introduced molecular and genetic marking methods as well as smaller sizes of transmitters for radio telemetry capable of tracking short-range movements of larger arthropods, accurate tracking of long-range movements and smaller arthropods is often difficult (Irvin et al. 2018, Fisher et al. 2021, Kral-O'Brien and Harmon 2021). For these difficult to track organisms, a pattern-based approach can therefore be advantageous.

One powerful pattern-based approach is analysis of the elements of metacommunity structure (EMS), three key metrics of species distribution across sites (coherence, species turnover, and boundary clumping) capable of distinguishing between several different theoretical patterns of metacommunity structure (i.e. checkerboard, nested subset, Clementsian, Gleasonian, evenly spaced, and random) (Leibold and Mikkelson 2002). The EMS framework examines a metacommunity as a site-by-species incidence matrix, which is then compared to null models and the 14 theoretical metacommunity pattern structures to determine the pattern that best fits the data (Presley et al. 2010). In this study, we take a pattern-based approach to analyze the metacommunity structure of herbivores and natural enemies in urban gardens in the California central coast. First, we use the EMS framework to identify the metacommunity patterns that represent the natural enemies and herbivores in our study region. We also quantify metacommunity structure as a gradient of change in species distributions across sites via a metacommunity matrix ordination. Next, we examine relationships between the quantified gradient of metacommunity structure and characteristics of local garden habitats and the urban landscape. Since herbivore communities are less likely to be limited by resources or competition due to high plant abundance in gardens, we predicted that herbivore metacommunity structure would be characterized by low species turnover in response to changes in environmental variation within sites. In contrast, natural enemy communities often include species with a variety of feeding strategies and dispersal ranges, so we predicted that natural enemy metacommunity structure would be characterized by high species turnover in response to environmental variation both within and among sites. Additionally, we hypothesized that garden and landscape characteristics contributing to ecological complexity (e.g. vegetation diversity and percent natural land cover respectively) would be associated with natural enemy and herbivore metacommunity structure.

Methods

Study system

We collected data at 24 community garden sites in the California central coast (Monterey, Santa Clara, and Santa Cruz counties) during the 2017 summer growing season (May through August). We selected garden sites that represent the distribution of land cover types surrounding cities in the central coast region, which includes intensive agriculture, coastal forests and grasslands, and urban green spaces. All gardens are organically managed in individual allotment plots or collectively, and sites are at least 2 km in distance from each other. At the time of study, garden sites had been cultivated between 2 and 50 years and ranged in size from 444m^2 to 15,400 m^2.

Arthropod sampling and identification

We sampled herbivores and natural enemies at each garden site at four sampling periods over the summer (May 15-19, June 19-23, July 17-20, and August 14-17), as previously reported in Philpott et al. (2020). We chose *Brassica oleracea* as a model system and focal crop for arthropod surveys because it is a common crop reliably found in garden sites throughout the season. We used a 20 x 20 m plot at the center of each site in which we haphazardly selected up to 20 *B. oleraceae* plants. To sample arthropods, we thoroughly inspected each plant by examining its leaves, stems, and fruits. We collected all arthropods encountered by hand using forceps and stored sampled arthropods in plastic vials containing 70% ethanol.

We identified sampled arthropods to morphospecies based on characteristic morphological features using dichotomous keys (Borror and White 1970, Marshall 2006) and online resources (Iowa State University Department of Entomology 2003, Favret and Miller 2014). We sorted arthropods into trophic guilds (e.g. herbivore, predator, parasitoid) according to diet and life history reported in identification resources.

Garden habitat and landscape characteristics

Concurrently with arthropod sampling, we surveyed garden canopy cover, vegetation, and ground cover within the 20 x 20 m plot. We used a concave spherical densitometer to measure canopy cover at five points (plot center and 10 m north, south, east, and west of center). We surveyed the woody vegetation in the 20 x 20 m plot by counting 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. Additionally, we counted the total number of *B. oleracea* plants in the plot, measured total garden size, and determined the age of each garden.

To survey herbaceous vegetation and ground cover, we used eight random 1 x 1 m quadrats within the 20 x 20 m plot. Within each quadrat, we identified all herbaceous plants to morphospecies, counted the number of flowers and plant species in flower, and measured the height of the tallest vegetation. We measured ground cover by visually estimating the percent of the quadrat covered by bare ground, grass, herbaceous plants, rocks, leaf litter, straw, and mulch or wood chips. We averaged vegetation and ground cover values for each site across the four sampling periods for all variables except one. For herbaceous plant species richness, we used all data to estimate the total herbaceous plant species richness (Chao 1) for each site across all sampling periods using the estimateR function in the 'vegan' R package (Oksanen et al. 2020, R Development Core Team 2021). We used natural-log (LN) and square-root (SQRT) transformations for variables that were highly skewed according to kurtosis and skew values. Thus, in total we collected data on 19 vegetation variables for each site, including mean canopy cover (SQRT), mean number of trees and shrubs, mean number of trees and shrubs in flower, mean number of tree and shrub species, mean number of tree and shrub species in flower, mean percent bare soil cover, mean percent grass cover (SQRT), mean percent rock cover (SQRT), mean percent leaf litter cover (SQRT), mean percent mulch cover, mean percent straw cover (SQRT), mean height of vegetation, mean number of flowers (LN), mean number of flower species, mean number of crop species, mean number of ornamental species (LN), mean number of weed species, and estimated herbaceous plant richness.

We used the 2016 National Land Cover Database (NLCD) to calculate the composition of land uses at 1, 2, and 5 km buffers around each site. We categorized land cover into four types: 1) natural (combining NLCD categories of deciduous, evergreen, and mixed forests; dwarf scrub; shrub/scrub; and grassland/herbaceous), 2) open (including NLCD values for lawn grass, park, and golf courses), 3) urban (including NLCD low, medium, and high intensity developed land), and 4) agriculture (including NLCD values for cultivated crops and pasture/hay). For each garden site, we measured the percent cover of each category and used the 'vegan' R package to calculate landscape diversity (modified Shannon-Wiener diversity index, *H*') within each buffer. In total, we measured 15 landscape variables and applied SQRT transformations to the following variables: natural land cover within 1 km, open land cover within 1 km, agriculture cover within 1 km, natural land cover within 2km, agriculture cover within 2 km, natural land cover within 5 km, open land cover within 5 km, and agriculture cover within 5 km.

Metacommunity structure analysis

We used the EMS framework to characterize metacommunities of 1) all herbivores, 2) all natural enemies, and 3) two individual natural enemy taxa (spiders and ants). The EMS approach examines patterns of species distribution across sites (as a site-by-species incidence matrix) and compares them to null models and theoretical pattern structures to determine the pattern that fits the metacommunity data (Leibold & Mikkelson, 2002). First, the metacommunity matrix is ordinated using reciprocal averaging, a method which groups together species with similar ranges and sites with similar species compositions. The theoretical pattern that best describes a metacommunity matrix is then based on analysis of three metrics: coherence, species turnover, and boundary clumping (Presley et al. 2010). We defined and evaluated these three metrics following Leibold and Mikkelson (2002) and Dallas (2014). Coherence measures the number of embedded absences in the ordinated metacommunity matrix. Non-significant coherence indicates random community assembly, while positive coherence indicates that most species in a community respond to environmental variation in similar ways and negative coherence suggests strong interspecific competition leading to competitive exclusion (checkerboard pattern). Turnover measures the number of times one species replaces another between two sites for each possible pair of species and sites. In other words, turnover is the rate at which species are lost and gained and can determine whether species turnover in response to environmental variation is individualistic (Gleasonian pattern) or synchronous (Clementsian pattern). Boundary clumping is the degree to which species ranges cluster together, which further differentiates among theoretical metacommunity patterns. Morisita's index of dispersion (I) is used to quantify boundary clumping, with I>1 indicating clumped species ranges and I<1 indicating over-dispersed ranges. We used the 'metacom' package in R to produce ordinated incidence matrices and calculate EMS metrics to determine the theoretical structure of each arthropod group (Dallas 2014). This process also allowed us to extract site scores based on the ordering of arthropod samples in metacommunity matrix ordination.

Relating metacommunity structure to garden habitat and landscape variables

Ordination of metacommunity matrices produces axes along which the distribution of species in a metacommunity are structured. The resulting ordination axes function as proxies of the combination of spatial, biotic, and abiotic factors that structure the metacommunity, effectively providing a latent gradient that can subsequently be analyzed to identify environmental variables associated with metacommunity structure (Presley et al. 2009, Dallas 2014). The EMS approach and canonical correspondence analysis (CCA) both use the same ordination method (reciprocal averaging), making them complementary methods for analysis of gradients structuring metacommunities (de la Sancha et al. 2014, Kim et al. 2021). For this reason, we chose to pair our EMS analysis with a CCA to assess garden habitat and landscape variables associated with the underlying metacommunity structure of each arthropod group.

To select variables for inclusion in the CCA, we first identified variables that play a role in structuring metacommunities based on correlations with site scores from the EMS analysis. We used Pearson's and Spearman's rank correlations testing for significant correlations between site scores and garden habitat and landscape characteristic variables for each arthropod group (Table 3.3). Using the resulting set of significantly correlated variables, we grouped variables into biologically relevant groups (e.g. vegetation variables, ground cover variables, landscape variables) and chose variables from each group that were not significantly correlated with each other. This process gave us a unique set of selected variables for each arthropod group. Additionally, we included garden size and age as selected variables for all arthropod groups due to their established importance in the urban landscape ecology of arthropods (Fattorini et al. 2018). We used the 'cca' function in the 'vegan' R package to implement a CCA assessing the local and landscape variables associated with the site score distribution, and thus the underlying metacommunity structure, of each arthropod group. As a check against collinearity, we evaluated the variable inflation factor (VIF) for each CCA, and all VIF scores were under 3. To identify environmental drivers of arthropod metacommunity structure, we evaluated associations between CCA axis 1 (which was highly correlated with EMS site scores) and selected garden habitat and landscape variables for each arthropod group.

Results

We sampled a total of 1,723 herbivores from eight species and 382 natural enemies from 42 species (Table 3.1). The most common herbivores were cabbage aphids (*Brevicoryne brassicae*, Hemiptera: Aphididae; n = 802, 46.5% of individuals sampled), silverleaf whiteflies (*Bemisia tabaci*, Hemiptera: Aleyrodidae; n = 232, 13.5%), and green peach aphids (*Myzus persicae*, Hemiptera: Aphididae; n = 165, 9.6%). Among natural enemies, the most abundant were aphid parasitoids (*Aphidius ervi*, Hymenoptera: Braconidae; n = 60, 15.7%), Argentine ants (*Linepithema humile*, Hymenoptera: Formicidae; n = 46, 12%), cobweb spiders (*Parasteatoda/Cryptachaea sp.*, Araneae: Theridiidae; n = 34, 8.9%), figitid wasps (*Alloxysta sp.*, Hymenoptera: Figitidae; n = 29, 7.6%), and convergent lady beetles (*Hippodamia convergens*, Coleoptera: Coccinellidae; n = 22, 5.7%).

EMS analysis revealed positive coherence across all metacommunities, indicating that all arthropod groups responded to environmental variation to some degree (Table 3.2). Turnover was positive for herbivores, spiders, and ants but negative for the group of all natural enemies considered together. Boundary clumping values were positive (Morisita Index > 1) for all groups, indicating that species ranges were clumped across arthropod groups. Following Presley et al. (2010), the metacommunity structure of all herbivores was best described as Clementsian while natural enemies exhibited a quasi-nested structure due to a non-significant turnover value. Spider metacommunity structure was quasi-Clementsian, and ant metacommunity structure was Gleasonian.

The CCA analysis showed that variation in metacommunity structure correlated with six garden habitat variables and four landscape variables across all arthropod groups (Table 3.4). The percentage of variance explained by the environmental variables (selected garden habitat and landscape factors) was 11.1% for herbivores, 9.8% for all natural enemies, 11.5% for spiders, and 27.5% for ants. The metacommunity structures of herbivores (Fig. 3.3a) and ants (Fig. 3.4b) were most highly associated with changes in landscape diversity at the 5 km scale, but no other variables explained significant fractions of the variation in herbivore metacommunity structure. Ant metacommunity structure was also highly associated with the percent urban land cover within 2 km. The metacommunity of structure of all natural enemies (Fig. 3.3b) and spiders (Fig. 3.4a), were most highly associated with the number of tree and shrub species in flower, a local garden habitat variable.

Discussion

In this study, we found that the metacommunity structure of arthropods in community gardens varies according to trophic group and in taxon-specific ways. According to EMS analysis, each arthropod group was characterized by a different theoretical metacommunity pattern. Paired with CCA results, we identified several garden local and landscape variables that may contribute to the assembly mechanisms proposed by the best fit theoretical metacommunity pattern. The metacommunity structures of all herbivores and ants were most strongly associated with characteristics of the landscape surrounding urban gardens, while the metacommunity structures of all natural enemies and spiders were most strongly associated with characteristics of the local garden habitat.

The herbivore metacommunity in our study region exhibited a strong response to environmental filters at the landscape level. According to EMS analysis, the metacommunity pattern of all herbivores was Clementsian, which is characterized by distinct community groups that vary in composition along an environmental gradient (Leibold and Mikkelson 2002). These distinct groupings are visible in the herbivore metacommunity plot, which shows that the three most common herbivores occur at most sites while a few herbivore species occur only at the extreme ends of the ordinated gradient of sites (Fig. 3.1a). Based on this analysis, herbivore metacommunities are likely structured by differential responses to environmental filters. One likely candidate for the environmental filter structuring the herbivore metacommunity is landscape diversity. As revealed by CCA, herbivore metacommunity structure was most strongly associated with landscape diversity within 5 km of garden sites, suggesting that herbivore community assembly depends on landscape complexity. Herbivore community composition thus changes with the number of land cover types surrounding gardens. Increasing landscape diversity near gardens provides a greater number of habitat types, including remnant natural and human-managed grassy spaces, which may reduce garden isolation from other green spaces in the landscape and facilitate herbivore migration for species with small dispersal ranges (Faeth et al. 2011). Landscape diversity is likely also associated with greater amounts of cultivated human greenspaces, such as roadways lined with trees and other vegetation, gardens, and residential yards. Studies of plant communities in cultivated urban greenspaces often find elevated plant species richness compared to remnant natural habitat (Hope et al. 2003, Avolio et al. 2020). High landscape diversity may therefore provide an abundance of plant resources for herbivores in cultivated, natural, and semi-natural habitats throughout the landscape. On the other hand, landscapes with fewer land cover types may provide fewer respites from impervious urban surfaces, which displace vegetation and produce heat island effects. Elevated temperatures associated with impervious cover have been associated with positive effects on some herbivores, including sap-sucking hemipterans like the aphids and whiteflies that were most common in our study, with hotter temperatures increasing their abundance and fecundity and reducing their mortality (Raupp et al. 2009, Meineke et al. 2013, Dale and Frank 2018). Landscape diversity may thus act as an environmental filter for herbivore communities, shifting community composition in response to species-specific responses to urbanization.

As a trophic group, the natural enemy metacommunity in our study region is likely structured by a mixture of spatial, biotic, and abiotic factors. Based on EMS analysis, the metacommunity structure of all natural enemies was best described as quasi-nested. A quasi-nested structure is similar to a nested subsets pattern, in which communities of fewer species form nested subsets of increasingly species rich communities, although nestedness may be less pronounced for quasi-nested communities (Leibold and Mikkelson 2002, Presley et al. 2010). Reflecting this structure, the metacommunity plot of all natural enemies depicts most of the species poor communities aligning with the upper end of the ordinated site gradient (Fig. 3.1b). Nestedness is common across ecological communities and can arise from sampling effects, extinction and colonization dynamics, as well as changes in habitat quality (Wright et al. 1998, Williams-Subiza et al. 2020). We did not directly measure biotic factors and no potential species traits or interspecies interactions are immediately apparent based on qualitative assessment of the metacommunity pattern of all natural enemies. However, the natural enemies present in our system are highly diverse, including 42 species, the most common of which only represented 16% of all individuals. Accordingly, these species encompass a range of body sizes, hunting strategies, and dispersal capacities, traits which likely play a role in producing this nested structure.

One abiotic factor that may be contributing to the nested structure of the natural enemy community is the number of tree and shrub species in flower. According to CCA, the number of tree and shrub species in flower was the garden characteristic variable most strongly associated with the natural enemy site score gradient. Flowering tree and shrub species contribute vegetation diversity, architectural structure, and floral resources that are relatively uncommon compared to extensive herbaceous plant cover in gardens. Conserving natural enemies in agroecosystems requires provision of a variety of resources, such as habitat refuges and alternative food and prey (Landis et al. 2000). Flowering tree and shrub species contribute floral resources, which provide nectar and pollen as alternative food resources and have been positively associated with natural enemy abundance in other urban gardens and farms (Lowenstein and Minor 2018). The number of tree and shrub species in flower was also correlated with the number of trees and shrubs and the number of tree and shrub species in our garden sites. Greater numbers of trees and shrubs and tree and shrub species may also create habitat microclimates, such as shady areas that promote cooler and wetter conditions. For instance, a previous study of urban street trees in North Carolina found that cooler temperatures can support retention of natural enemy species that are sensitive to urban heat, such as ghost spiders (Meineke et al. 2017). In general, natural enemies are more abundant under conditions of high habitat structure and vegetation complexity (Langellotto and Denno 2004). For these reasons, some natural enemy species may only be present in garden communities when particular resources, such as flowering tree and shrub species, are present.

The structure of the spider metacommunity in our region appears to be driven by environmental filtering based on garden habitat suitability. EMS analysis showed that the metacommunity pattern that best described spiders was quasi-Clementsian, which shares the same Clementsian characteristics described above except that its positive species turnover is not statistically significant (Presley et al. 2010). Species turnover was marginally significant for the spider metacommunity ($p = 0.082$), and the metacommunity plot shows a similar pattern to the herbivore metacommunity, with four distinct clumps of species groups partitioning themselves along the site gradient (Fig. 3.2a). One possible factor driving environmental filtering of spiders is the number of trees and shrubs in flower, which was the variable most highly associated with the spider CCA axis. While spiders do not eat flowers, flowering trees and shrubs may attract spider prey items and, in turn, the spider species that hunt them (Rebek et al. 2005). Plants that are taller and larger in biomass have been associated with a greater abundance of large-bodied spiders and a lower abundance of small, web-building spiders in urban green spaces (Delgado de la flor et al. 2020). Changes in vegetation biomass, such as provided by trees and shrubs, could alter the spider species present in garden sites and shift spider metacommunity structure. Previous studies have also found positive associations between spider abundance and species richness, flowering plant species diversity, and total vegetation cover in urban green spaces (Otoshi et al. 2015, Lowe et al. 2018). In our garden sites, spider community composition may thus shift in response to changes in the availability of resources and hunting niches provided by flowering tree and shrub species.

The ant metacommunity in this region is likely structured by a combination of biotic factors (e.g species interactions) and abiotic factors (e.g. urban landscape composition). The metacommunity structure of ants was Gleasonian, indicating change in species composition along an environmental gradient with individualistic distribution of species ranges on that gradient (Leibold and Mikkelson 2002). As evident in the ant metacommunity plot, ant species largely did not co-occur across sites (Fig. 3.2b). *L. humile,* the invasive Argentine ant, had the largest species range while all other ant species had much smaller ranges. Considering the abiotic factors that we measured, CCA showed that ant metacommunity structure was most highly associated with two landscape variables, landscape diversity within 5 km and urban cover within 2 km. Urbanization can be considered as a type of disturbance that has species-specific effects on ant communities (Perfecto and Philpott 2023). Studies of urbanization often report negative effects on ant species richness and abundance (Buczkowski and Richmond 2012), although at least one study showed ant diversity peaking at intermediate levels of urbanization followed by declines in species richness at high levels of urbanization (Sanford et al. 2009). Urbanization is associated with several factors that can favor nonnative ants and generalist ants capable of exploiting urban resources, including access to buildings that can provide shelter from inclement weather; water, nesting sites, and abundant mutualists in irrigated greenspaces; and food from human garbage (Vonshak and Gordon 2015). In contrast, some native ants are completely absent from urban sites while others can adapt to urban settings (Vonshak and Gordon 2015). These variable responses of ants to urbanization (urban exploitation, avoidance, and adaptability) may underlie the importance of urban land cover and landscape diversity in shaping ant metacommunity structure in our study.

While Gleasonian metacommunities are typically not defined by strong interspecies competition (Leibold and Mikkelson 2002, Presley et al. 2010), the qualitative pattern of the ant metacommunity suggests that a biotic factor, namely interspecific competition, may also be contributing to ant metacommunity structure. In some studies, nonnative ant abundance in urban settings has led to interspecific competition between native and nonnative ant species and overall reductions in ant species richness (Suarez et al. 1998, Uno et al. 2010). Negative impacts of Argentine ants on native ants have been documented in California (Suarez et al. 1998, Egerer et al. 2017a), although at least one other study has failed to document an impact on native ants nearby our study region (Clarke et al. 2008). Of the ant species documented by this study, only one (*Monomorium ergatogyna*) is native to California (Holway 1999), suggesting that most native ants in the region avoid urban areas. To facilitate species coexistence among remaining species, urban ants can utilize heterogeneity in habitat, including differences in temperature, shade, and impervious cover, coupled with their own nutritional preferences (e.g. optimal protein:carbohydrate ratio of foods) to carve out non-overlapping ecological niches, facilitating species coexistence (Stahlschmidt and Johnson 2018). The Gleasonian metacommunity pattern we observe here may thus arise from individualistic species responses to intensive urban development and number of land cover types in the landscape surrounding gardens, with species inhabiting unique niches according to differences in ability to disperse and exploit urban habitat fragments, rather than strong interspecific competition. For instance, studies of the Argentine ant in Southern California have found that Argentine ant abundance and invasion success is highly dependent on irrigation and associated wet conditions, while native ants have more variable responses to irrigation (Menke and Holway 2006, Menke et al. 2007). On the other hand, this finding may also reflect the outcome of long-term competitive exclusion by the Argentine ant, as has been reported in coastal Southern California (Achury et al. 2021). Legacy effects of interspecific competition with Argentine ants in the past may thus result in other ant species occurring only in habitats that are not suitable for Argentine ants.

Overall, our results show that herbivore and natural enemy metacommunities are shaped by habitat and landscape characteristics in distinct ways. All arthropod groups had coherent metacommunity structures, indicating that each group responds to a common environmental gradient (Samu et al. 2018). Herbivore, spider, and ant metacommunities were also characterized by positive turnover, which suggests a strong influence of environmental variability on species composition via habitat filtering (Mihaljevic et al. 2015). One possible explanation for the lack of positive turnover in the natural enemy metacommunity is that this trophic grouping represents a diverse group of species with various foraging strategies and life histories, potentially obscuring responses of individual natural enemy guilds. Additionally, some of the natural enemy taxa represented in the all natural enemy metacommunity (but not abundant enough to analyze individually), such as lady beetles and parasitoids, are highly mobile and may experience high permeability of the urban landscape with few dispersal constraints. For instance, a previous study of lady beetles in this system found no significant impact of geographic or spatial distance on lady beetle community composition (Liere et al. 2019). Comparing the metacommunity structure of herbivores and natural enemies, herbivore structure was most highly associated with landscape structure whereas characteristics of the local garden habitat had a strong influence on the structure of natural enemies as a trophic group and one natural enemy taxon (spiders). This result suggests that the urban landscape may be more permeable for natural enemies, many of which are highly mobile compared to herbivores (Raupp et al. 2009, Egerer et al. 2017a), leading to greater discernment of local habitat quality by natural enemies. Natural enemies may also have less consistent responses to urban landscape composition due to differences in diet specialization and matrix tolerance. Matrix intolerant species are not able to survive outside of their preferred habitat patches and thus depend on the connectivity of suitable habitat patches, while matrix tolerant species can survive the matrix and be more widespread throughout the urban landscape (Burkman and Gardiner 2014).

These results suggest a few implications for community gardeners wishing to utilize biological pest control in their gardens. First, the composition of herbivore pests encountered by gardeners will likely depend on the location of the garden in the urban landscape. The large impact of landscape diversity on herbivore metacommunity structure suggests that the regional species pool of herbivores is filtered by landscape composition according to herbivore species traits, such as dispersal, and tolerance to urban microclimatic conditions, such as urban heat (Raupp et al. 2009). Gardeners may thus be able to tailor biological control efforts to the specific herbivore pests that predominate at their specific garden site. In contrast, gardener management decisions, such as including more flowering tree and shrub species, may have a greater impact on the composition of natural enemy species throughout the region. Strategies to attract and retain natural enemies may thus be more generalizable across community garden sites. Coordinated efforts across garden sites to increase the amount of natural enemy resources provided by individual garden sites may help ensure the persistence of natural enemies across the study region.

One caveat of this study is that the proportion of variation explained by constrained variables (the garden habitat and landscape variables used here) in CCA was low across all arthropod groups, indicating that garden habitat and landscape variables account for a small amount of the variation in metacommunity structure of arthropods in community gardens. The variables measured in this study most directly consider the influence of abiotic variation in gardens and the urban landscape. The qualitative metacommunity patterns we observed suggest that biotic factors, such as interspecies interactions (for ants) and prey availability (for all natural enemy groupings), may be important for our system as well. Additionally, it is possible that other environmental conditions common in cities that we did not measure here, such as the age of cities, air pollution levels, pesticide and herbicide applications in managed green spaces, and the urban heat island effect, may also be affecting urban arthropods and their interactions with plants and other arthropods in ways that extend to metacommunity structure (McIntyre 2000, Aronson et al. 2017, Miles et al. 2019, Fenoglio et al. 2020). Further, while biophysical factors of urban landscapes play a role in explaining distributions of arthropods in gardens, recent work has pointed out the importance of explicitly considering the social factors that shape human management of the composition and spatial configuration of urban habitat patches (Andrade et al. 2021). For instance, social dynamics such as mimicry and social norms can foster homogeneity in management of urban patches. On the other hand, differences in financial resources, neighborhood demographics, and landholder priorities can produce heterogeneity in urban patch management (Andrade et al. 2021). Incorporating landscape-level social factors in addition to the local-level differences in human habitat management studied here could therefore provide a fuller understanding of the metacommunity dynamics of urban arthropods.

Conclusion

Urban community gardens can function as habitat patches connected by arthropod migration within a matrix of inhospitable urban environments (e.g. impervious surfaces). Taking a metacommunity approach, this study examined the metacommunity structure of four arthropod groups: herbivore and natural enemy trophic groups as well as two natural enemy taxa, spiders and ants. Further, by pairing the elements of metacommunity structure framework with a canonical correspondence analysis, we identified characteristics of garden habitat and landscape context that contribute to the metacommunity structure of these arthropod groups. Taken together, our results suggest that the garden herbivore metacommunity is shaped by the composition of the surrounding landscape to a larger extent than garden habitat characteristics, whereas the natural enemy metacommunity is largely shaped by garden habitat variables. However, metacommunities of different natural enemy taxa, such as the spiders and ants studied here, can be structured and affected in distinct ways depending on the traits, dispersal ranges, and foraging strategies represented by each taxon group as well as interspecies interactions within those groups. Future studies may wish to additionally consider other relevant groupings of natural enemy species (e.g. specialist vs. generalist species, flying vs. walking species) to provide a more detailed understanding of the local and regional dynamics of important natural enemy species in urban gardens and the biological pest control they support.

Table 3.1 Arthropods (herbivores, natural enemies) sampled in urban gardens in the California Central coast. Four-letter species codes are given for each morphospecies.

Trophic group	**Order**	**Family**	**Morphospecies**	**Species Code**
Herbivores	Coleoptera	Chrysomelidae	*Diabrotica undecimpunctata*	DIUN
	Diptera	Bibionidae	*Dilophus sp.*	DISP
	Hemiptera	Aleyrodidae	*Bemisia tabaci*	BETA
		Aphididae	*Brevicoryne brassicae*	BRBR
			Myzus persicae	MYPE
		Pentatomidae	*Chinavia hilaris*	CHHI
			Murgantia histrionica	MUHI
	Lepidoptera	Pieridae	*Pieris rapae*	PIRA
Natural enemies	Araneae	Anyphaena	Anyphaena sp.	ANSP
		Araneidae	Araneus gemma	ARGE
			Araneus sp.	ARSP
			Zygiella/Parazygiella	ZYPA
		Eutchuridae	Cheiracanthium sp.	CHSP
		Linyphiidae	Erigone dentosa	ERDE
			Erigone sp.	ERSP
			Microlinyphia sp.	MISP
			Neriene sp.	NESP
		Oxyopidae	Oxyopes sp.	OXSP
		Salticidae	Phidippus sp.	PHSP
			Sassacus sp.	SASP
		Tetragnathidae	Metellina sp.	MESP
			Tetragnatha sp.	TESP
		Theridiidae	Latrodectus hesperus	LAHE
			Latrodectus sp.	LASP
			Parasteatoda/ Cryptachaea sp.	PACR
			Steatoda nobilis	STNO
			Steatoda sp.	STSP
			Theridion sp.	THSP
	Coleoptera	Coccinellidae	Coccinella californica	COCA
			Coccinella septempunctata	COSE
			Cycloneda polita	CYPO
			Cycloneda sanguinea	CYSA
			Harmonia axyridis	HAAX
			Hippodamia convergens	HICO
	Hymenoptera	Braconidae	Aphidius colemani	APCO
			Aphidius ervi	APER
		Figitidae	Alloxysta sp.	ALSP
			Alloxysta brassicae	ALBR
		Formicidae	Cardiocondyla mauritanica	CAMA
			Linepithema humile	LIHU
			Monomorium ergatogyna	MOER
			Nylanderia vividula	NYVI
			Tetramorium caespitum	TECA
			Unknown GenSp	FOUN
		Pteromalidae	Pachyneuron aphidis	PAAP
			Pteromalidae Unknown GenSp	PTUN

Table 3.2 Results of analyses of coherence, species turnover, and boundary clumping for arthropod metacommunities in urban community gardens in the California central coast.

	All herbivores	All natural enemies	Spiders	Ants
Coherence				
Absences	107	1,025	226	0
Z-score	-8.23	-7.14	-6.51	-3.38
p-value	<0.001	<0.001	<0.001	<0.001
Sim mean	401	1,608	524	57
Sim SD	36	82	46	17
Turnover				
Replacements	1,160	46,818	11,679	301
Z-score	4.21	-0.906	1.74	2.8
p-value	<0.001	0.365	0.082	0.005
Sim mean	359	55,585	8,457	114
Sim SD	190.5	9,682	1,854	67
Boundary clumping				
Morisita Index	4.14	2.1	2.69	1.83
p-value	0.009	<0.001	<0.001	0.19
df	90	80	55	32
Metacommunity structure	Clementsian	Quasi-nested, clumped species loss	Quasi-Clementsian	Gleasonian

Table 3.3 Pearson's correlations (*r*), Spearman's rank correlations (*ρ*), and associated p-values for correlations between metacommunity site scores (extracted via reciprocal averaging) and significant garden local and landscape characteristic variables. 'LN' indicates natural-log transformed variables and 'SQRT' indicates square root transformed variables. '*' denotes variables included in canonical correspondence analysis.

Taxon	Significantly correlated variables	Pearson's correlations		Spearman rank correlations	
		r	p-value	*ρ*	p-value
All herbivores	# Trees and shrubs*	-	-	0.32	0.002
	# Trees and shrubs in flower	-	-	0.23	0.028
	# Tree and shrub species richness	-	-	0.23	0.027
	Natural land cover (5 km)	-	-	0.21	0.047
	Urban land cover (5 km)	-	-	-0.2	0.051
	Landscape diversity (5 km)*	-	-	0.23	0.03
All natural enemies	# Trees and shrubs in flower	0.28	0.012	-	-
	# Tree and shrub species in flower*	0.29	0.008	-	-
	Rock ground cover (1 m, SQRT)*	0.36	<0.001	0.32	0.003
	Straw ground cover (1 m)	0.25	0.021	-	-
	Natural land cover (1 km)*	0.23	0.04	-	-
	Agriculture land cover (2 km)	-	-	-0.24	0.027
	Agriculture land cover (5 km)*	-	-	-0.28	0.01
	Landscape diversity (5 km)*	-	-	-0.22	0.042
Spiders	# Trees and shrubs in flower	0.3	0.023	-	-
	# Tree and shrub species in flower*	0.29	0.025	-	-
	Rock ground cover (1 m)	0.35	0.007	-	-
	Bare soil (1 m)*	-	-	-0.29	0.025
	Natural land cover (1 km, SQRT)*	0.26	0.053	-	-
Ants	Garden size (LN)*	0.34	0.043	0.5	0.002
	# Trees and shrubs*	-0.34	0.047	-0.31	0.066
	Rock ground cover (1 m, SQRT)*	0.37	0.029		
	Natural land cover (1 km)	-0.36	0.033	-0.42	0.011
	Open land cover (1 km, SQRT)	-0.5	0.002	-	-
	Urban land cover (1 km)	0.42	0.012	-	-
	Natural land cover (2 km, SQRT)	-0.45	0.007	-0.49	0.003
	Open land cover (2 km)	-0.59	<0.001	-0.45	0.007
	Urban land cover (2 km)*	0.57	<0.001	0.58	<0.001
	Natural land cover (5 km, SQRT)	-0.6	<0.001	-0.43	0.01
	Open land cover (5 km, SQRT)	-	-	-0.44	0.009
	Urban land cover (5 km)	-	-	0.61	<0.001
	Agricultural land cover (5 km, SQRT)*	-	-	-0.59	<0.001
	Landscape diversity (1 km)	-0.54	<0.001	-	-
	Landscape diversity (2 km)	-	-	-0.47	0.005
	Landscape diversity (5 km)*	-0.59	<0.001	-0.56	<0.001

Table 3.4 Contribution of garden habitat and landscape variables to first axis of canonical correspondence analysis (CCA). Values shown are the loading value of the first CCA axis. Bolded values indicate high level of correspondence (<0.5) between CCA first axis and garden habitat and landscape variables. 'LN' indicates natural-log transformed variables and 'SQRT' indicates square root transformed variables.

Variable	**All herbivores**	**All natural enemies**	**Spiders**	**Ants**
Garden size (LN)	0.432	0.106	-0.287	0.457
Garden age	0.313	-0.109	**-0.536**	0.042
# Trees and shrubs	-0.47	-	-	-0.318
# Trees and shrub species in flower	-	**-0.74**	**-0.678**	-
Bare soil ground cover			-0.072	-
Rock ground cover (SQRT)	-	-0.488	-	0.443
Natural land cover (1 km, SQRT)	-	-0.245	0.03	-
Urban land cover (2 km)	-	-	-	**0.706**
Agriculture land cover (5 km, SQRT)	-	0.039	-	-0.391
Landscape diversity (5 km)	**-0.813**	-0.192	-	**0.708**

Figure 3.1 Visualization of ordinated metacommunity matrices of arthropod herbivores (A) and natural enemies (B) found in community garden sites in the California central coast. Black rectangles indicate species (columns) occurrence at a site (rows). See Table 3.1 for species codes.

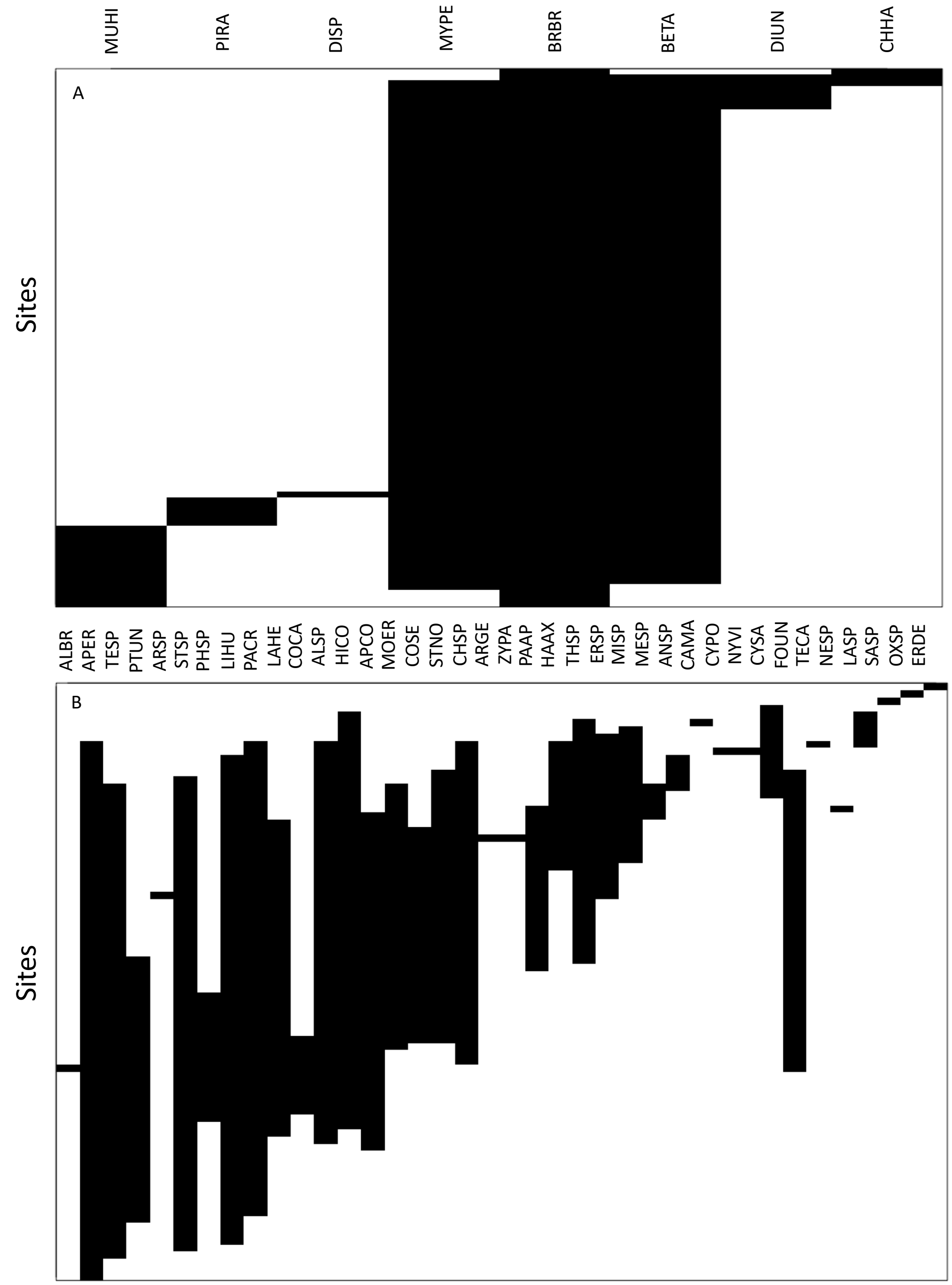


Figure 3.2 Visualization of ordinated metacommunity matrices of spiders (A) and ants (B) found in community garden sites in the California central coast. Black rectangles indicate species (columns) occurrence at a site (rows). See table 3.1 for species codes.

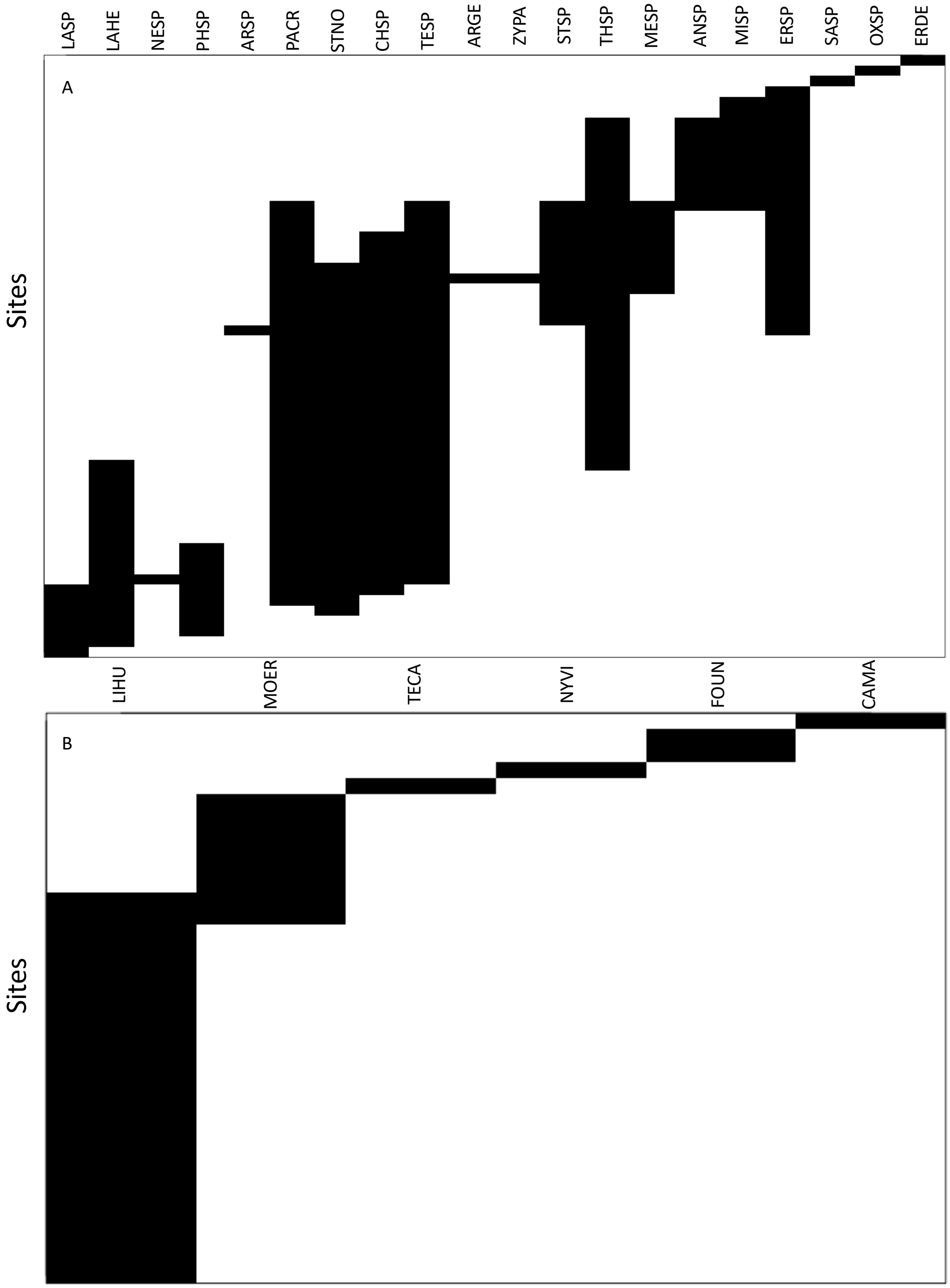


Figure 3.3 Canonical correspondence analysis (CCA) bi-plots of arthropod herbivores (A) and natural enemies (B) found in community gardens in the California central coast. Species scores from CCA are plotted along first and second axes of ordination. Arrows represent vectors of garden habitat and landscape variables and point in the direction of their highest values. Arrow lengths are proportional to their importance in explaining variation in metacommunity structure. See table 3.1 for species codes.

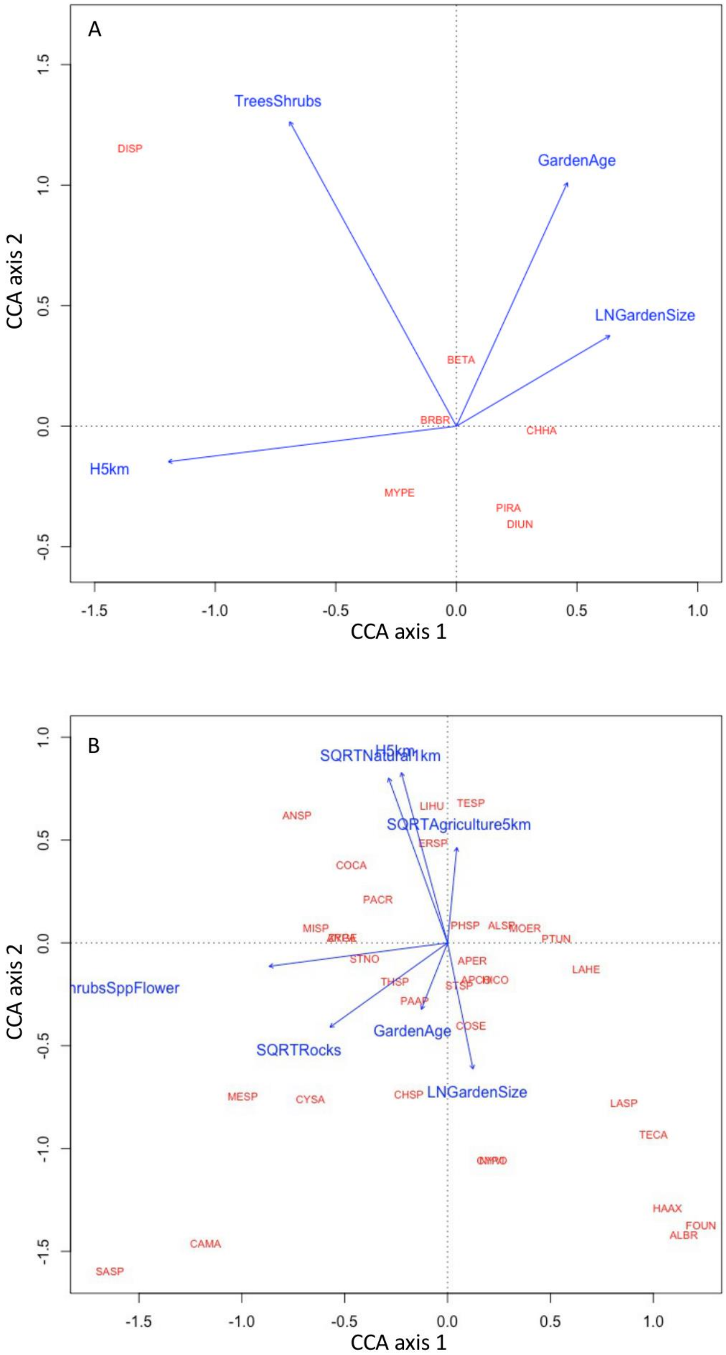
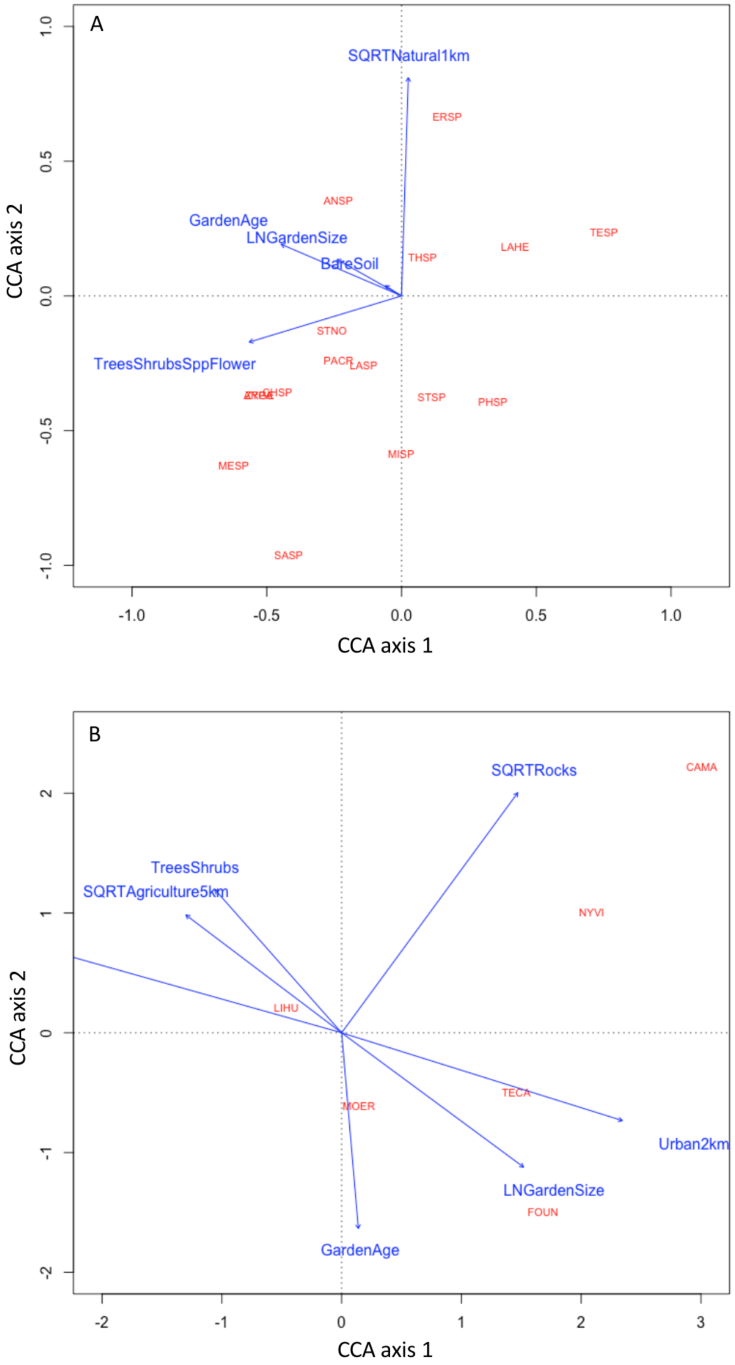


Figure 3.4 Canonical correspondence analysis (CCA) bi-plots of spider (A) and ant (B) metacommunities found in community gardens in the California central coast. Species scores from CCA are plotted along primary and secondary axes of ordination. Arrows represent vectors of garden habitat and landscape variables and point in the direction of their highest values. Arrow lengths are proportional to their importance in explaining variation in metacommunity structure. See table 3.1 for species codes.



CHAPTER 4: Socio-ecological processes producing gradients of garden complexity

Abstract

Despite the benefits of ecological complexity, preferences for tidy and generally ecologically simple cultivated landscapes are the norm in both rural and urban settings. As urban agroecosystems, community gardens have roots in several lineages of landscapes aesthetics, spanning conventional and sustainable agriculture and various forms of urban greenspaces. According to Bourdieusian theories, tidiness in rural agricultural fields is upheld as an aesthetic norm through a shared cultural *habitus* among farmers. In parallel, urban yard owners are expected to subscribe to tidy lawn maintenance, a practice intended to produce upstanding, moral urban citizens. Urban garden plots exhibit a range of management styles that can similarly speak to the values of urban gardeners and urban garden projects more broadly. Drawing on focus groups and semi-structured interviews with community gardeners in the California central coast, I investigate differences in gardener aesthetic preferences and management priorities to understand how they manifest in garden plots. By examining garden plot styles on an aesthetic spectrum ranging from tidy to wild, I show how the choices community gardeners make to conform with or diverge from the tidy aesthetic norm lead to variation in ecological complexity in community gardens.

Introduction

Ecological complexity in agroecosystems is characterized by the integration of various forms of agricultural biodiversity, such as the inclusion of multiple crops with complementary ecological functions in the traditional milpa system of corn, beans, and squash. Complex agricultural systems are often associated with higher levels of biodiversity and ecosystem function, providing bountiful harvests, resources for wildlife, and allowing for reduction or replacement of synthetic inputs like pesticides and fertilizers (Altieri 1999, Vandermeer et al. 2010). Yet, studies of landscape aesthetics in the United States and many European countries have documented strong preferences for tidy agricultural landscapes, the largely monocultural fields of a single crop that are relatively simple ecologically (Nassauer 1988, Burton et al. 2008, Sutherland and Darnhofer 2012, Saunders 2016). Tidy agricultural landscapes are often characterized by orderly rows, dense crops, and an absence of weeds. The preference for tidiness is especially prominent among farmers, who have frequently been found to associate tidy agricultural landscapes with proper care for land, efficiency, productivity, and good citizenship (Nassauer 1988, Burton 2012). Tidiness is thus a powerful shared aesthetic that informs socially acceptable agricultural practices and likewise dictates practices that are not acceptable. In some instances, environmentally protective practices that appear messy or unproductive, such as participating in payments for land restoration, can fall outside the tidy aesthetic and generate resistance to conservation practices (Burton et al. 2008). Farmer aesthetic preferences are not static and can shift over time, such as when farmers transition from conventional to organic farming (Sutherland and Darnhofer

2012). Further, the practices, skills, and knowledge that make up accepted aesthetic norms in agricultural management are often dependent on socio-ecological contexts governing specific environmental regions and agricultural commodities.

Community gardens are an interesting case to consider here because they are at the intersection of rural and urban agricultural traditions and are thus informed by various lineages of landscape aesthetics. Urban gardens have been present in U.S. cities since about the 1880s in response to working class struggles in industrializing cities, such as unemployment, food insecurity, and public health challenges (Bassett 1981). Many early urban garden projects sought to instill civic values and a strong work ethic in urban residents, imbuing the systematic and orderly design of these gardens with a sense of morality and civic purpose (Bassett 1981). This history of orderly and neat landscape aesthetics in urban agriculture persists into the present. Tidiness is widely recognized as a cue for human caretaking of land (Li and Nassauer 2020), and many urban residents report preferring tidy gardens and other urban greenspaces (Lindemann-Matthies and Brieger 2016, Laage-Thomsen and Blok 2021). A second strand of aesthetic influences lies in sustainable agricultural practices. Modern community gardens are motivated in part by an awareness of the destructive environmental consequences of industrial agriculture as well as a desire for access to fresh foods grown close to home (McClintock 2010). For this reason, many urban gardeners use a variety of sustainable growing practices, which can be simple—such as when substituting synthetic inputs for organic inputs—or can be complex, intricate, and holistic shifts in the ways gardens are managed—such as increasing plant species richness, infrequent weeding, or soil disturbance. Sustainable practices that introduce ecological complexity can be unattractive to some gardeners but aesthetically appealing to others (Beck et al. 2002, Lindemann-Matthies and Marty 2013), with implications for the implementation of ecological complexity in urban gardens. A third strand of landscape aesthetics informing community gardens is the multi-cultural composition of the gardener population. Community gardens often provide space for gardeners to reconnect with traditional agricultural practices from their cultural heritage or country of origin (Saldivar-Tanaka and Krasny 2004, Mares and Peña 2010), leading to the comingling of diverse reference points for garden landscape aesthetics each with their own rich histories.

In the California central coast, community gardens include a wide range of aesthetic preferences and management priorities. Demographically, the gardener population in this region is highly diverse. A 2017 survey of 185 gardeners revealed that participants spoke 21 languages, represented 36 nationalities, ranged in age from 22-91, had incomes spanning from no income to over $250,000 a year, and education levels ranging from no formal education to doctorate (Egerer et al. 2018b). Survey respondents also reported a variety of motivations for gardening, including access to food, opportunities for recreation, and connections to nature and social community (Philpott et al. 2020a). Visually, gardener plots span a gradient from very tidy and manicured plots to messier, wild plots (pers. obsv). While the tidy and wild extremes of the aesthetic spectrum coexist in community gardens, they generate varying perceptions among urban residents. Further, the management considerations and values that underlie the two different aesthetics from the perspective of community gardeners have yet to be explored.

This study examines the social-ecological processes that produce gradients of ecological complexity in community gardens. I investigate the values that inform garden management decisions and how gardeners communicate these values in the aesthetics of their plot. First, I situate community gardens within the context of aesthetic norms governing cultivated landscapes in rural and urban settings. Then, I use evidence from focus groups and semi-structured interviews to argue that "tidy" and "wild" garden aesthetics differ in the values they prioritize. I find that wild garden plots can disrupt the dominant aesthetic norm of tidy garden plots in community gardens and help diversify the ecological habitat, resources, and function provided by community gardens. However, gardener preferences for tidiness or wildness do not necessarily conform to particular production logics (i.e. productivist or sustainability-oriented approaches to urban agriculture).

The *habitus*, cultural capital, and rural agricultural landscape aesthetics

While farming practices are highly pragmatic and shaped in large part by the pressures of capitalist production, agricultural management is not immune to the influence of social norms. Burton analyzes farmer aesthetic preferences through Bourdieu's concept of the *habitus*, the collection of socialized norms and tendencies that guide behavior and thinking (Bourdieu 1977). Bourdieu describes the *habitus* as an internalized scheme determining how individuals perceive, understand, and act within their social world. The *habitus* is shaped by participation in a specific social group, such as a social class or field of work, and imbues individuals with a particular world view that values certain social and cultural ideas. Possession of valued material and immaterial attributes confers cultural capital, the social assets (e.g. skills, tastes, and embodied knowledges) individuals accumulate by conforming to the status quo of their social group (Bourdieu 1986). Burton contends that farmer preferences for tidy agricultural landscapes are the product of a shared cultural *habitus* (2012). Aesthetic evaluation of agricultural landscapes therefore involves a process of social judgement decoding the knowledge and skills on display in the agricultural landscape. Agricultural landscapes are shaped by everyday farming practices and thus reflect the knowledge, values, and work ethic of the farmer. As demonstrated by Nassauer's work with farmers in Illinois, farmers often interpret tidiness as a form of care, noting and acknowledging the work that goes into maintaining neat fields (1988). According to Burton et al. (2008), maintaining a reputation as a "good farmer" amongst a peer group of farmers provides cultural capital. One important marker of good farming is efficiency, manifesting as regular and tidy fields, which has become embedded in a *habitus* with a preference for tidy landscapes (Nassauer 1988, Burton 2012).

Research into farming aesthetics has often revolved around integrating conservation practices in agricultural landscapes, which can entail a departure from the tidy, productivist aesthetic. For example, land that is set aside for restoration of wild plants can appear "scruffy" to farmers, and the effectiveness of the conservation work can be difficult to judge based on appearance (Burton et al. 2008). Nassauer

(1988) notes that some farmers differentiate between landscape choices that would appear beautiful to the general public, such as flowering weeds with pink flowers, and the clean landscapes that are attractive to farmers. Participating in environmental schemes can result in a loss of cultural capital for farmers, which disincentivizes voluntary adoption of these schemes. Burton et al. (2008) argue that, as a result of the loss of cultural capital, passive, land sparing approaches to conservation are unlikely to become integrated into the cultural *habitus* of farmers and be widely adopted. A more compatible approach would be promoting conservation practices that mimic the production of cultural capital in conventional agriculture and provide farmers greater agency, such as using measurable species conservation targets that reward higher levels of species conservation which could then be compared among farmers. Sutherland and Darnhofer (2012) complicate this representation by noting that Burton's conceptualization of how farmers generate cultural capital presupposes stable "rules of the game," or in other words, the set of norms and behaviors associated with a specific field that allow for reliable symbols of cultural capital. However, the context of farming and the rules of the game have changed substantially in recent decades, with growing concerns about the sustainability of agricultural practices becoming embedded in societal expectations and market demands. For instance, the rise of organic agriculture and shifting agricultural policy in the European Union have created dynamic rules of the game, leading to a gradual process of negotiation and expansion of the symbols of cultural capital valued by farmers (Sutherland and Darnhofer 2012). Accordingly, Saunders' work with Swedish farmers shows that new symbols of good farming, such as animal welfare, have begun to emerge among some farmers, although many farmers continue to associate organic and sustainable practices with inefficiency and a lack of productivity (2016).

In addition to changes in the economic and political context of agriculture, the social identity of farmers can also influence notions of good farming and resulting agricultural landscapes. For instance, farmer gender can impact how farmers perceive and value tidy agricultural fields. In a study of Irish farmers, Burns (2021) found that men ascribed high value to tidiness and engaged in harsh judgment of other farmers based on the tidiness or untidiness of their fields. In contrast, women farmers did not participate in criticism of other farmers based on the tidiness of their fields, although many women did appreciate tidiness and acknowledged that tidiness conferred respect. Women farmers were also more likely to express sympathy for farmers with untidy farms, considering that the age or health of farmers might impede them from maintaining tidy fields (Burns 2021). In Riley's work on farmer age and tidiness, a study of farmers continuing to work over the age of 65 in the United Kingdom found that older farmers valued a tidy farm appearance and prioritized high visibility and managerial tasks to maintain their good farmer status (2016). Despite having less stamina or physical strength, older farmers continued to tap into the cultural capital of the good farmer by utilizing detailed, site-specific knowledge they had built up over time to keep up with the tasks that contribute the most to cultural capital (Riley 2016).

Few studies have considered the influence of race or class on ideals of good farming and landscape aesthetics, but Ofteshage notes that the values and symbols of good farming often assume whiteness and benefit from the exclusion and dispossession of marginalized groups (2022). For instance, Canadian settler claims that indigenous lands were incompetently managed and cultivated were historically used as justification for indigenous land dispossession and continue to inform farmers' perceptions of indigenous peoples and their land rights (Rotz 2017). Williams' study of the American south of the 1950s and 60s shows that "clean fields" and "clean cotton" denoted weed-free fields as well as an absence of black workers, who at that point had been replaced by agricultural mechanization and chemical herbicides (2020). Legacies of exclusion from land ownership continue to maintain low numbers of farmers of color, which may be one reason why few studies have focused on their perspective to date. Race and class likely shape farmer conceptualizations of good farming and their manifestation in agricultural landscape aesthetics in interesting ways that deserve future study. Urban gardens are a good location to address this gap in the literature because, compared to rural farmers (although not farmworkers), urban gardener populations tend to be less overwhelmingly white.

Cultivating and codifying tidiness in urban landscape aesthetics

In urban and suburban settings, tidiness continues to be an entrenched value in cultivated urban green spaces, and this is perhaps most evident in the production of turfgrass lawns. The modern American lawn has its roots in English landscape traditions of the eighteenth century, a style first transplanted to American colonial gardens and eventually becoming a mainstay of middle-class suburban regions (Butler-Bowdon 2001). In their original European context, open grass meadows and lawns connoted idyllic ideals of paradise that over time became tied to the wealth and privilege of the aristocracy’s manor homes and the significant labor required to maintain turfgrass (Robbins 2012). Similar to conventional agricultural fields, modern tidy lawn maintenance requires high inputs of herbicides, fertilizers, and pesticides as well as regular mowing (Robbins and Sharp 2003). Perhaps more unique is the fervor with which lawn tidiness is upheld. While many farmers interpret tidiness predominantly as a reflection of the quality of farm work and the work ethic of the farmer, tidy lawn care is often considered a manifestation of the morality and strength of character of the yard owner. As Robbins (2012) traces, the moral values of carefully maintained grass lawns follows the aesthetic concerns of American urban park design in the nineteenth century, which sought to provide urban dwellers access to groomed and civilized grassy spaces in contrast to the ruggedness and disorder of both natural and urban landscapes, environments which were thought to foster moral indecency. With the spread of grass lawns to the growing suburbs in the postwar era, private lawns became a means for creating an upstanding moral citizenry. It is within this social context that mutual observation, social pressure, and disciplinary action via residential or municipal authorities continue to be deployed to monitor and enforce the modern tidy lawn aesthetic (Robbins et al. 2001, Sisser et al. 2016). This level of surveillance is possible due to the high visibility of lawns. Rather than producing food, grass lawns are cultivated landscapes that are meant to be displayed, rendering visible to urban residents the labor and practices that maintain the lawn. In surveys, urban residents have articulated that lawn maintenance habits reflect the character and civic virtue of the yard owner, especially in wealthy neighborhoods where conforming to the tidy lawn aesthetic can also contribute to high property values (Robbins et al. 2001). Under this shared social and economic understanding, the practices and patterns of consumption that make the tidy lawn aesthetic possible are normalized.

The value of tidiness in urban cultivated landscapes is persistent but not unchallenged. In parallel to concerns about the environmental sustainability of conventional agricultural practices, the value of the perfectly uniform, green lawn has begun to be questioned by some yard owners and alternatives are gradually emerging. Among urban residents, there is growing recognition that grass lawns are not well suited to supporting biodiversity (Campbell-Arvai 2019). In response, some urban residents are beginning to add ecological resources for wildlife to their yards, such as flowering and fruiting plants, native plants, and trees and shrubs (Goddard et al. 2013). However, Goddard et al. (2013) show the majority of yard owners continue to prefer neat and tidy yards, so provision of resources for wildlife may have to be balanced with maintenance of neighborhood standards and expectations of tidiness. One way yard owners in Chicago appear to have achieved this balance is by concentrating wildlife resources in back yards, which are generally less visible than front yards (Belaire et al. 2016). In regions with water scarcity, conservationists have advocated for xeric, or low-water use, landscaping in residential yards, and some households have followed suit. In a study of households in Missouri, Fan et al. found that yard owners with especially high and especially low incomes were more likely to adopt drought tolerant plants, suggesting that both high and low access to financial resources can motivate urban residents to transition away from turfgrass lawns (2017). However, long-time residents as well as residents of older neighborhoods in the semi-arid region of Phoenix were more likely to stick to turfgrass, further indicating that traditional grass lawns still have a strong hold on the landscape choices of urban residents. Thus, despite the private ownership of yards, social norms and expectations exert a strong influence on whether and how households integrate wildlife-friendly resources and climate adaptations to diversify their yards.

In contrast to private residential yards, communally managed urban gardens can foster resistant uses of urban land and alternative landscape aesthetics. Urban garden projects can diverge from capitalist modes of production and valuation when they are committed to sustainable and just food systems or reclaiming urban space for marginalized communities (Galt et al. 2014). In their study of Puerto Rican community gardens in New York City, Saldivar-Tanaka and Krasny (2004) found the composition of garden crops and built structures reflect the culture and indigenous ancestry of the largely Puerto Rican gardeners, creating Latinx-coded agricultural and social spaces used for community celebrations and cultural events often tied to Puerto Rican agricultural practices. Immigrant community gardens can thus re-embed the social relations between people and land severed by migration from their homelands. In Los Angeles, Mares and Peña (2010) show that gardeners at the

South Central Farm collectively constructed an autonomous space supporting the local immigrant community by appropriating urban land for kitchen gardens grown using traditional plants and practices from their home countries. Many South Central Farm gardeners used living fences of cacti, sugarcane, banana, and avocado to delineate garden parcels and the perimeter of the larger garden, tapping into a common element of the landscape aesthetics of rural areas of northern Mexico (Mares and Peña 2010). Since these living fences are used for organization, one could argue that they add tidiness to the urban landscape, but only in the eyes of urban residents for whom this version of tidiness is legible.

The legibility of the alternative aesthetics of urban agriculture often depends on the identity and resources of those mobilizing spaces for urban agriculture. In the case of the South Central Farm, race- and class-based barriers to the political and cultural capital required to legitimize the garden and gardeners' claims to urban space led to the garden's destruction in 2006 (Barraclough 2009). Conversely, the largely white population of "eco-conscious" urban gardeners in a small town in Michigan used their political and economic relations to combat concerns about the perceived messiness of permaculture-style gardens by invoking the environmental benefits of these gardens (Maurer 2021). Urban agriculture predates the tidy lawnscape in this town, but urban residents who kept vegetable gardens in the early twentieth century did so for subsistence reasons and tended to be poor and black. Residents who experienced social mobility quickly abandoned their vegetable gardens and adopted turfgrass lawns as a class signifier (Maurer 2021). Maurer argues that the race-class positionality of contemporary white urban gardeners allowed them to align with the moral authority of the emerging green middle class to win policies supporting and protecting urban agriculture. Similarly, Glennie (2020) shows that Seattle's P-Patch community gardening program has been safeguarded and legitimized in large part due to leadership from white advocates and program staff. Despite the multiculturalism of the P-Patch program's gardener membership and the promotion of this diverse population as a justification of the public benefits of community gardens in Seattle, participation in the program has not directly granted marginalized gardeners access to political resources to leverage for related urban concerns, such as gentrification and displacement of low-income families (Glennie 2020). Thus, urban gardeners with access to power and resources are better equipped to bypass the established aesthetics of urban landscapes and begin to normalize or reappropriate alternative aesthetics, as long as the alternative aesthetics do not disrupt the status quo.

In the context of the California central coast community gardens, gardeners can cultivate their own version of tidiness. Previous observations of these community gardens indicate that gardeners produce a range of visual aesthetics through their choice of plant species and gardening strategies (e.g. how plants are arranged, how often the garden is weeded). On visits to the gardens for ecological field work, some gardeners have expressed self-consciousness about their own perception of the unkemptness of their garden while other gardeners do not seem perturbed if their garden appears messy (pers. obsv). Similar aesthetic differences, with some garden plots appearing neat and tidy and others less so, have been documented in community gardens in Singapore and the Netherlands (van den Berg and van Winsum-Westra 2010, Montefrio et al. 2020). In the present study, I investigate the extent to which gardeners' choices about what and how they grow are guided by a cohesive aesthetic vision. Further, I ask whether garden aesthetics are tied to distinct production logics (i.e. productivist gardens focused on maximizing harvests or sustainability-oriented gardens that prioritize the health of the garden ecosystem). As reviewed above, the values shaping cultivated landscape aesthetics have been extensively explored in rural farms and urban residential yards, but few studies have focused on the landscape aesthetics of community gardens. This study contributes to scholarship on urban agriculture and landscape aesthetics by examining potentially competing landscape aesthetics and values among community gardeners as well as their implications for both urban residents and urban biodiversity. The results identified and interpreted here indicate that social norms encourage maintenance of tidy garden plots over wild plots. However, gardeners with diverging aesthetic preferences and management priorities are willing to break with the tidy norm, presenting viable alternatives for caretaking garden plots that may better support the diverse needs of urban residents and biodiversity.

Methods

This research took place over the summer and fall of 2021 and the winter and spring of 2022. I used a combination of focus groups and semi-structured interviews to gather data. I used flyers posted in gardens and emailed by garden managers to recruit gardeners from 25 community gardens located in Santa Cruz, CA and San Jose, CA. A total of fifteen community gardeners from 7 different garden sites participated in this study, with seven gardeners taking part in the focus group and eight gardeners completing an interview (Table 4.1). Focus group participants included mostly white women, while interviews were able to capture more diversity in gender, race and ethnicity, and nationality, including Asian and Latino gardeners. There was a spread of education and income levels. Across the two groups, two thirds of participants were from gardens in Santa Cruz and one third were from gardens in San Jose. Participants either chose or were assigned a pseudonym, and I changed all names and places mentioned in transcripts to protect participant confidentiality.

The focus group took place over Zoom from September to November 2021. I met with the seven participants at seven one-hour meetings to carry out a photovoice project (Wang and Burris 1997, Sutton-Brown 2014). At the first meeting, I reviewed the research protocol, obtained informed consent, and collected socio-demographic information from participants using a Qualtrics survey. For the second meeting, I facilitated group discussion of participant growing practices, management preferences, and interactions with wildlife in the garden. The third meeting consisted of a training on the basics of photography for research, including tips for composing photographs and ethical considerations in selecting photography subjects. I also presented participants with three photovoice prompt assignments informed by their previous group discussion and solicited feedback on the prompts before providing instructions for responding to each prompt with a captioned photograph. The three prompts were: 1) what does your ideal garden plot look like, 2) what does a big challenge in your garden look like, and 3) what does an instance of harmony or conflict in your garden look like? Participants shared and discussed their photographs with each other at the fourth, fifth, and sixth meetings (Fig. 4.1-3). At the final meeting, I presented a summary of the photovoice responses and requested feedback on my preliminary interpretations of the data as well as potential avenues for disseminating the results to the public. I saved audio-recordings of each Zoom meeting with consent from participants.

Since the virtual setting and time commitment required to participate in the focus group presented a barrier to entry for many gardeners, I carried out additional semi-structured interviews with eight gardeners aiming to cover the same discussion topics addressed in the focus group. Interviews took place from January to March 2022 in the modality preferred by each participant (in-person at the community garden or over Zoom). I used an interview guide with questions on four topics: participant demographic information, gardening background and motivations, management preferences, and interactions with garden biodiversity. Interviews lasted between 30 to 90 minutes, and I audio-recorded each interview with consent from the participant. I conducted six interviews in English and two interviews in Spanish.

I transcribed focus group meetings and interviews by first generating an automatic transcription of audio files using Yuja software. I then corrected each transcription by listening back to the audio to compare the accuracy of each line of the transcript. For the two interviews in Spanish, I manually transcribed and translated each interview myself. To code and analyze my data, I used a thematic analysis approach. Thematic analysis is a flexible, inductive method for systematically identifying, organizing, and interpreting patterns or themes across a data set (Braun and Clarke 2012). Following this approach, I first familiarized myself with the data through several rounds of reading to observe any possible themes relating to my research questions or consistent with previous literature. I then coded for words or phrases indicating the aesthetics, management styles and priorities, and relations to wildlife reported by participants. For photovoice responses, I analyzed photographs and captions alongside transcripts from group discussion, but I focused on transcript data to accurately represent participants' interpretations of their photos and captions.

Values informing garden management and aesthetics

I found several shared aesthetic values among community gardeners: abundance/productivity, tidiness, organization/design, beauty/attractiveness, and sustainability. The value most universally cited as desirable was garden abundance and productivity. Gardeners described this as plots that were verdant, with many different plants and big harvests, usually summer gardens. Gardeners often expressed this value when describing their motivations for gardening, which commonly included taking enjoyment in watching plants grow and learning about their life cycles. For example, one interview participant explained the meaning behind abundance in their garden:

> There is a small desire to like have successful vegetables grow from the plants that we grow. Like I want a sense of success, not necessarily high-yield, like lots of vegetables, but like, I want us to have a value. And so often that conversation ends up being not about like, oh my gosh, we got 12 plants or 12 tomatoes off this plant. It's more like, wow, we really learned something about this plant growth so that the product of it is a delight (Avery, interview).

Some gardeners also described garden abundance in relation to their mental health, which verdant plots supported by providing access to nature. The opportunity to spend time with plants outdoors was especially important for urban gardeners who did not otherwise have access to land in expensive rental markets. Garden plots with abundant produce show the fruits of a successful season of gardening, and many gardeners enjoyed being able to share their bounty with others:

> And, you know, it’s something I can share with other people too. Like when I have an overabundance of like lettuce, I can offer my colleagues at work. Hey, I have more than I need. And so being able to give it away, like, provide for other people too, is also an added benefit that, you know, we all like those feel good feelings, right? (Kim, interview).

Additionally, productive gardens conveyed a high level of knowledge and skill, which was often sought out by novice gardeners who wanted advice from more experienced gardeners. Thus, abundant harvests and the knowledge and skill required to produce these harvests may contribute to a positive reputation and social standing among gardeners that can extend to other urban residents through gifts of produce.

The second most common desirable aesthetic was garden tidiness. Tidy gardens were often described as “clean,” with no weeds and neat rows. Several gardeners expressed a strong preference for tidiness: “I do like my garden to look very neat…I think it just looks nice if it’s tidy. I can't bear to see the weeds coming up. That bindweed, my enemy” (Betty, focus group meeting 2). Several gardeners who cultivated tidy plots elaborated that tidiness was the product of the hard work of weeding, which can be a time consuming and physically demanding process. One gardener asserted that tidiness was an indicator of proper soil and plant preparation that supported plant vigor, growth, and productivity (Cesar, interview, translated from Spanish). As with conventional agricultural fields and manicured lawns, tidiness thus communicates the labor and consistent care that a gardener puts into their plot and can be a source of pride for some gardeners. Surprisingly, tidiness was recognized as valuable even by some gardeners who did not maintain tidy plots: “I don't think my own personal garden will ever be nice, neat rows, but I do admire it when I see it" (Kat, focus group meeting 4). Thus, garden plot tidiness was considered aspirational for many gardeners across the tidy and wild plot management style spectrum. While this study did not directly evaluate factors that contribute to cultural capital, gardener responses suggest that tidiness is an important element of maintaining a reputation as a “good gardener.”

A related but separate aesthetic value was garden organization and design. Many community garden plots are small, so plots that are well planned and organized make good use of the limited space and are easier to water and harvest, as one gardener explained:

> I have a very small plot, 200 sq ft. And I tend to plant in rows. But I’ll plant rows depending on the height of the vegetable. One that's growing taller, will shade something that'll grow less than height. And I tend to plant two rows close together, and then a walkway, and then two rows close together, so I can harvest from every other row. So space accommodation is critical in my garden because I plant year-round. I harvest year-round (Aesir, focus group meeting #2).

As this quote hints at, garden organization also accounts for the biophysical and microclimatic conditions of the plot, which can vary from plot to plot. A key consideration for most gardeners was keeping track of the sunny and shady zones in their plot. Patterns of sunlight and shade impact solar radiation and moisture levels, which determine what plants gardeners can grow and where plants with certain growing requirements need to be placed. Some gardeners, like Cynthia and Felicia, planned their gardens out in great detail, systematically mapping out the composition and organization of each garden bed with timelines for rotating plants in and out. Other gardeners, like Millie and Kim, took a more haphazard approach that prioritized getting plants in the ground wherever there was appropriate space for them. Additionally, protective design choices, such as using gopher wire and gating with locked doors, were also desirable for some gardeners. One participant, Sukie, attributed problematic location and open design to the frequency of theft and destruction in her original plot of ten years. The original plot had no fencing and was next to a highly trafficked pathway in her neighborhood. When a plot further away from the pathway with more protective features, including a fence and a lockable gate, became available, she quickly moved to take it over:

> I was eavesdropping when someone said, ‘Oh, we're really going to miss you’. This woman who put in this plot that I'm in now. And I said, ‘miss you?’ She's leaving? Because I witnessed what she did. She had somebody come in and just put gopher wire in the whole plot area and then put weed cloth down and then build the raised beds on top of that and put gopher wire under it. And I was like, I want that plot, I want that plot, I want that plot. So I called the city, and I said, is she really moving? And he said yes. And I said, can I move there? So I moved there last year (Sukie, focus group meeting 4).

Thus, well organized and designed plots can stand out and be highly desirable for some gardeners for practical as well as aesthetic reasons.

Gardeners also valued the aesthetic beauty and attractiveness of specific garden elements that they chose to include in their plots. For many gardeners, plots were also recreational spaces that they enjoyed making comfortable and beautiful. Some gardeners integrated decorative elements such as archways, pathway stones, and sculptures. One gardener described her experience turning her garden into a refuge during the initial outbreak of the COVID pandemic:

> My ideal garden started with the garden table and chairs…I enjoy spending time in the garden, writing, painting, drawing, planning, enjoying a cup of tea… So, taking in the sights and sounds, especially on a day that is misty or foggy (Artsy, focus group meeting 4).

Garden beauty may thus be especially important for gardeners who spend more time in the garden or who enjoy bringing their creativity into the garden. Several gardeners described taking joy in the natural beauty of things that grow in the garden, such as colorful flowers and varieties of crops. For instance:

> I like having a lot of flowers and prioritizing that and getting joy from that versus having this, like…I had this weird crotchety old farmer approach of like, why would I need a flower when I just need to eat (Cynthia, interview).

Cynthia’s initial hesitation around planting flowers suggests that the beauty of the garden can be secondary for gardeners who prioritize other garden aspects, like abundant produce. Previous research from this system suggests that women are more likely to plant flowers and other ornamental plants (Philpott et al. 2020a), so valuing garden beauty may also be dependent on gardener gender.

Most gardeners valued the sustainability of their plots, but this value could take on different aesthetic forms. The community gardeners here are all required to use organic practices, as dictated by rules governing these community gardens. At minimum, this means not using synthetic fertilizers, pesticides, or herbicides. Beyond these ground rules, some gardeners have further interests and commitments to sustainable practices. Most commonly and visibly, gardeners reported cover cropping, companion planting, rotating crops, and using native plants to promote pollinators. A few gardeners mentioned having released natural enemies, like lady beetles, in attempts to control pests. Some gardeners used regenerative soil practices, such as no-till and other practices that minimize soil disturbance and build soil health. In focus group meetings, several participants recognized the sustainable practices at work in other gardeners' photographs, confirming the visibility of sustainable growing practices and suggesting the presence of a sustainability aesthetic. While some of these practices can be integrated into plot management in tidy and organized ways, this is not always the case. One gardener with a strong stated commitment to sustainable practices in both her garden and her life described her gardening approach:

> My thoughts on that are just to keep things growing in the most healthy way possible. Rather than having it look a particular way. I guess that's my style of gardening there. Yeah, I don't think it looks so beautiful (Cav, focus group meeting 2).

Cav's explanation demonstrates how gardeners who prioritize sustainable growing practices can deviate from the tidy aesthetic norm. For gardeners like Cav, strong sustainability values may also legitimize opting out of the imperative to consider the aesthetic presentation of gardening choices to instead prioritize the ecological and environmental functions supported by the garden plot.

The final value I describe is wildness, a somewhat subversive value that is not formally encouraged but that persists to varying degrees among gardeners. Gardeners often framed wildness in contrast to tidiness. For instance, several gardeners expressed their preference for the wild look of plants that were allowed to organically mix together instead of being planted in neat rows or blocks. Wildness also described the overgrowth of crops and other intentionally cultivated plants, including plants often considered weeds. One gardener explained how wildness provided a more flexible approach: “You don't always want to have like a precision. I want to be able to let my hair down a little bit (Millie, interview).” Flexibility of time was especially important for gardeners who had to juggle caring for the garden with other commitments, such as caring for children or keeping up with the demands of their jobs. For some gardeners, wildness itself was an appealing aesthetic while other gardeners considered wildness the result of disorder in their garden, as one gardener explained:

> We don't really plan the layout. I sort of picture this garden as all over the place. Um, we start with good intentions of like, okay, we'll put things in a certain area. And it doesn't always work very well…It’s not really our forte. So yeah. Sort of a little bit of a wild garden jungle in terms of where things are. (Kim, interview).

Whether intentional or not, wildness could be understood as a product of reigning in the intensity of human management or influence over the growth of the garden plot.

In the remainder of this paper, I focus on the distinctions between tidy and wild aesthetics because these were the main ways gardeners characterized the overall aesthetic style of their gardens. Of the gardeners represented in this study, eight gardeners had plots that they described as tidy and seven gardeners described their plots as wild. Considering these styles as part of a spectrum from extremely tidy to extremely wild, three participants were far to the tidy side, four were pretty far on the wild side, while the remaining eight participants were somewhere in between.

The tidy aesthetic norm

After garden abundance, tidiness is the predominant aesthetic norm in the gardens, and tidiness is encoded to a degree by garden rules. The seven community gardens represented by participants are all run by the Parks and Recreation departments of the City of Santa Cruz and the City of San Jose, which both set expectations for garden maintenance that trend toward tidiness. Gardens in San Jose have extensive and detailed rules prescribing how gardens should be maintained, including mandates to weed, trim, and actively maintain the garden year-round (San Jose Parks Recreation & Neighborhood Services 2022). Further guidelines detail planting schedules, percentages of the plot area that must be planted, and maximum heights for plants. Emanuel, a participant from a San Jose garden, commented on the burdensome number of rules that must be followed: “There are many rules, too many. Well, the garden rules that come from the city. Every year we have to fill out a contract and we must follow certain rules. And of course, the rules are obeyed”

(Emanuel, interview, translated from Spanish). Community gardens in Santa Cruz similarly stipulate that gardeners must keep pathways clear of plants, prevent plants from getting too big, and keep plots free of weeds (Avery, interview). However, several Santa Cruz participants reported that these rules are not actively enforced. These differences in enforcement suggest that gardeners have more flexibility to explore alternatives to the tidy aesthetic in Santa Cruz, and accordingly departures from the tidy norm were more common among participants from gardens in Santa Cruz. The proximity of hubs for agroecology and sustainable agriculture in Santa Cruz may contribute to an environment where gardeners are more amenable to shifts away from the tidy norm and where garden managers are open to a range of garden caretaking levels.

In addition to formal garden rules, informal monitoring of garden aesthetics contributes social pressure to conform to the tidy aesthetic norm. The proximity of garden plots facilitates mutual observation amongst gardeners, which participants at times utilized to learn from others and at other times to critique other gardeners. While focus group participants generally expressed appreciation for the differences in aesthetic styles they all represented, one participant implied that his tidy weed management was simply a matter of greater discipline and better time management compared to his neighbors:

> I noticed this morning the gardens adjacent to me are covered with weeds, particularly after this recent rain last week. Yeah, it's just covered with weeds and management is a little bit lax on encouraging people to eliminate the weeds. So I have weeds all around me. It's just that my garden, I take a few minutes, and it doesn't take but a couple of minutes to run around and knock anything or everything down before I leave (Aesir, focus group meeting 6).

Among interview participants, one mentioned receiving unsolicited comments from a neighboring gardener:

> My neighbor here, I asked him one year to water for me because we were going away. And he's like, 'you're like a guerrilla gardener, like it's just like a guerrilla warfare gardening.' He wasn't criticizing me. I think he was, like, humorous. That he was saying it's just like so overgrown and like kind of wild (Millie, interview).

Millie's neighbor may have been poking fun, but his statement indicates that some gardeners may regard plots that are not orderly and tidy as illicit to some degree. This view is supported by Millie's own observation of gardens that crossed a threshold from messy to neglected: "The weeding does not get enforced. And you're supposed to use the garden. And actually, that really makes me annoyed when people have a plot year after year and they don't use it or they barely use it" (Millie, interview). At multiple points in our interview, Millie vacillated between wishing her garden looked neat and tidy and asserting her preference for a more "organic" look that requires less "precision." For instance:

> So the person next to me, their garden's like really manicured and like they have a plan, you know, every year. It's very nice. And while I like and want to do that sometimes, it's just not who I am (Millie, interview).

Gardeners' scrutiny of themselves and others suggests that they participate in an aesthetic gaze, a form of diffuse power that Montefrio et al. (2020) describe as an extension of the panopticon gaze where a particular aesthetic and associated conduct are normalized and individuals participate in surveilling and disciplining their own and others' conduct. In gardens where formal rules are not routinely enforced, the influence of the aesthetic gaze may urge gardeners to keep their gardens tidy.

Departing from the tidy norm—integrating "wildness"

The tidy garden norm imposes an aesthetic that is not always compatible with the values, goals, and time availability of gardeners, leading to contestation of this norm. Of the fifteen gardeners who participated in this study, eight described their aesthetic as mostly tidy and seven had plots they considered wild or messy. Several wild plot gardeners shared the sentiment that the tidy, highly manicured aesthetic was too constricting and that they preferred other reference points or aesthetic models for their own gardens. For example, Millie referenced the influence of English gardens, "where it's like different textures and sizes and kinda like maybe more permaculture [that] kinda goes into the surrounding area more" (Millie, interview). Cynthia, a wild plot gardener with a more organized approach to wildness described a neighbor's less organized wild plot as "Alice in Wonderland-style" and "exploding with life" (Cynthia, interview). Jorge, a wild plot gardener originally from Peru, mentioned the influence of having grown up near the Amazon rainforest and explained his preferred aesthetic: "Ideally, for me, I guess I like a total chaos environment…I'm not too attracted when it's too clean-cut…and life out there for them, in the real world for the plant, it's not a clean-cut environment" (Jorge, interview). Thus, while garden tidiness can signal order and discipline, wild plot gardens tap into an alternative value of closeness to nature, which can be especially valuable in the urban context these gardens inhabit. Access to urban nature can be low for many urban residents, especially considering inequitable distributions of urban nature (Keeler et al. 2019, Colding et al. 2020). Moreover, most common urban green spaces, like parks, tend to be managed and ordered by people. Space for urban nature that is less ordered and more spontaneous is limited beyond residential homes, and garden plots thus provide a rare space of agency for urban residents who value wild forms of urban nature.

Both tidy and wild plot styles are on a spectrum, and some participants shared that either extreme could be off-putting. Felicia, a participant with an organized and tidy plot, shared her insight into plots that she considered too tidy:

> I don't need it to be super manicured. Some of the plots here are super manicured. I think some people call one of the plots, like the person, Mr. Pristine (Felicia, interview).

Besides Felicia, one other tidy plot gardener and one wild plot gardener noted plots that they perceived as overly manicured as something to avoid. While some gardeners evidently prefer a hyper tidy aesthetic, gardeners with aesthetic preferences closer to the middle-ground of the tidy and wild spectrum may perceive the tidy extreme as excessively fussy and artificial. Felicia's reference to "Mr. Pristine" also indicates that plot management style can create a reputation for gardeners linked to their plot's appearance, recalling the social dynamics of mutual observation and judgement among farmers and lawn owners (Robbins et al. 2001, Burton 2012). On the other end of the spectrum, gardens that were overly wild were perceived as neglected or abandoned by both tidy and wild plot gardeners. For instance, one wild plot gardener observed, "If you look around, there are many garden beds here that are just totally overrun with weeds. And I don't think they really care" (Cynthia, interview). Similarly to those managing farm and yard landscapes, community gardeners thus actively evaluate plot maintenance and management style gradients, ascribing perceived values and personality traits to their neighbors.

While wild plots may appear unkempt and neglected to gardeners with an eye for the tidy aesthetic, wild plot gardeners make informed, purposeful decisions about how they manage their plots. Wild plots arguably make use of ecological processes like succession that occur over longer timescales and that tidy garden plots typically exclude. For example, one key feature of wild plots is the inclusion of “volunteer” plants. Gardeners described these as edible or otherwise useful weeds that sprout up in the garden on their own and that gardeners choose to keep in their plot. Gardeners are often very knowledgeable about the plants that occur naturally in the garden, and wild plot gardeners reported using this knowledge to curate their selection of volunteer plants. Further, wild plots often included overgrown plants that gardeners allowed to grow beyond their typical harvest time and go to seed, which gardeners often saved for the next year’s planting. Some wild plot gardeners also prioritized soil regeneration and below-ground processes that could appear untidy above-ground. For instance, Cynthia maintained a large section of her plot that she called “the grave,” where she accumulated leaf litter and other dead plant matter so that it would decompose and build soil fertility (Cynthia, interview). Above ground it appeared untidy, but below ground she was intent on turning it into “a gold mine.”

Contrary to the association with messiness, wild plots followed their own organization schemes that varied in levels of detailed planning. Cynthia described creating an ordered flow for her plot by using highly detailed plans for each bed, which allowed her to experiment with different growing strategies in a systematic way (Cynthia, interview). Millie preferred a more flexible approach, working in smaller sections of her plot in a more spur of the moment way (Millie, interview). For Millie, this was a more manageable approach that allowed her to better juggle the demands of caring for her garden and two young children. Similarly, Jorge admitted that “sometimes the garden becomes, uh, a second priority” during busy periods in his family life (Jorge, interview). As Jorge indicated, wildness in garden plots can occur temporarily when gardeners were too busy to consistently work on their plots. This allows plants to follow their own course of growth without intervention from the gardener. Jorge described this as plants “resisting” the tidy norm over time as they become more established, attracting more insects and birds (Jorge, interview). However, Jorge also described taking seasonal breaks from the garden as a strategic way to avoid peak gopher activity in his plot. Thus, wild plot gardeners asserted their own pace for managing garden plots that prioritize their own life rhythms.

In addition to aesthetic and time management considerations, wild plot gardeners often articulated a strong sense of environmental responsibility informing their appreciation for wildness in their gardens. This pattern aligns with previous studies reporting an association between environmental education and a preference for wildness in urban and residential green spaces (van den Berg and van Winsum-Westra 2010, Zheng et al. 2011, Hwang et al. 2019, Hu et al. 2022). While concern for the environment was not exclusive to wild plot gardeners, wild plot gardeners often discussed formal or informal environmental education in relation to their garden practices. Most wild plot gardeners reported engaging in informal environmental education tied to gardening, such as researching sustainable growing practices by seeking out online and text resources. In terms of formal education, one wild plot gardener, Cynthia, referenced being interested in community gardening because of their association with local, sustainable agriculture and her exposure to environmental research through university studies. Two wild plot gardeners additionally mentioned family members who worked on or studied environmental topics. One of these gardeners, Millie, described her experience learning at home with her child during the height of the COVID pandemic:

> I had my kid at home and we had to supplement a lot. We just really got into different subjects that I hadn't spent time really learning about like fungus and like diving deeper. There's a lot of cool research coming out…I don't think there's a day that's going by that I'm not reading about plants, animals, and mushrooms and insects. And like, I'm not always reading about it from the gardening lens, but it's all connected because gardens are out in nature (Millie, interview).

Overall, environmental education may provide an additional justification for wild plot gardeners to feel comfortable diverging from the tidy aesthetic. In Singapore, where the tidy aesthetic is heavily enforced in urban gardens, gardeners in school gardens incorporating permaculture added signs to educate the public about the scientific basis of the wildness to excuse the perceived messiness of their gardens and attempt to increase their social acceptability (Montefrio et al. 2020). Environmental education amongst community gardeners here may similarly help diminish social barriers to breaking with the tidy norm.

Finally, wild plot gardeners had their own limits on how much wildness they allowed in their plot, since these are still human managed agroecosystems. Wild plot gardeners often acknowledged the practical challenges associated with wildness:

> I will say it's kind of a balance because it’s harder to water when everything is wild and not in rows. I had to go away a couple of times over the summer, and I felt bad for the people taking care of my plot because, you know, it was just a lot more challenging to water it. So I have to figure out, like, a balance there (Kat, focus group meeting 2).

Wild plot gardeners described several indicators that it was time to intervene and cut back on the amount of wildness in their garden, such as when plants got too prickly and difficult to deal with, when plants got too tall and began shading neighboring plots, and as a matter of safety for young children who could scratch and hurt themselves in dense foliage. Despite these challenges, wild plot gardeners recognized the value of wildness in their plots, whether due to aesthetic or management preferences, and chose to accommodate wildness in their plots.

Approaches to wildlife

While gardening styles primarily deal with choices about plants in the garden plot, gardens provide habitat for many kinds of wildlife that gardeners may try to attract or attempt to deter with their gardening choices. Surprisingly, whether a gardener maintained a tidy or a wild plot aesthetic did not predict any particular wildlife management approach. Most participants were observant of diverse forms of wildlife in their plots, supporting the idea that participation in urban agriculture can foster biophilia (Lin et al. 2018). Tidy and wild plot gardeners alike were interested in supporting beneficial species, such as pollinators, earthworms, and natural enemies, as well as charismatic species like birds. One notable exception was a tidy plot gardener, Cesar, who was adamant about not wanting any kind of animals in his plot because they could damage his plants (Cesar, interview).

When it came to pest or nuisance species, plot management style was also not associated with wildlife management approaches, as gardener stances were more individual. For example, gophers are the most cited problem species in the region due to their destructive tunneling in garden plots, and participant stances toward gophers ranged from intolerance to coexistence. Most commonly, participants exhibited some level of intolerance for gophers and employed a variety of strategies to get rid of gophers. Some participants used the especially aggressive tactics of trapping and killing gophers, while others experimented with natural gopher deterrents like hot sauce and coyote pee. Participants with more tolerant stances tended to use gopher wire to line the bottom of garden beds, preventing gophers from tunneling inside. One participant, Cynthia, had mixed feelings about using gopher wire, explaining that she preferred a more hands-off approach:

> I always try to think like, okay, how can I do the most minimal way I can and like work with this? Because if it's here, it's part of a larger system that maybe I can control parts of, but maybe I can't control. And there's always a cost. There's always a cost to management (Cynthia, interview).

Two participants, Jorge and Emanuel, shared a stance of coexisting with the gophers, stating that the gophers were a natural part of the environment and that the garden was their home. The lack of agreement between tidy and wild plot gardeners may speak to the fact that these style differences deal more directly with how gardeners manage the plants in their plot rather than how they relate to wildlife.

Management aesthetics and sustainability

Considering the full spread of participants in this study, I found that tidiness was not necessarily mutually exclusive with a sustainability orientation and wildness was not always the product of sustainability values. Instead, both tidy and wild garden styles were able to be paired with gardening priorities that leaned productivist or leaned toward sustainability. Most gardeners were motivated by producing food, and tidy plot gardeners were often especially interested in the productivity of their plants. However, several tidy plot gardeners were committed to sustainable practices but typically chose practices that fit within the dominant tidy norm because they enjoyed that aesthetic. One wild plot gardener, Kim, specifically prioritized abundant food production but explained that her garden appeared messy and wild because she often struggled to fit in visits to her garden and was too busy to plan her garden out in detail (Kim, interview). Most gardeners expressed some level of interest in sustainable growing practices, but two wild plot gardeners, Cav and Cynthia, explicitly stated that they prioritized the sustainability and health of their garden over the amount of food they produced. Unlike agricultural fields and residential yards where management styles tend to be quite homogenous, variability is more common in community garden management, likely because the people managing garden plots are more diverse than the populations of farmers and yard owners that have been studied previously. Rather than directly aligning with production priorities, garden management styles therefore represent the many values and constraints that community gardeners express through their garden plots.

Finally, I turn to the ecological implications of these different plot styles. Both tidy and wild plots use organic management, but wild plots may provide additional resources and habitat that are less common given the dominance of tidy gardens. For example, tidy plots are heavily weeded, which decreases vegetation diversity. Wild plot gardeners also weeded their gardens, but they reported curating a wider selection of plants by choosing to leave in volunteer plants and large, past-harvest plants. For these reasons, plant diversity and structural complexity tends to be relatively higher in wild plots. Wild plot gardeners were also more likely to use practices like no-till that appear unsightly aboveground but promote biodiversity belowground. Comparatively, wild plots may thus have higher plant diversity and belowground diversity. Overall, gardeners who are uncompromisingly committed to the tidy aesthetic may lose out on opportunities to build ecological diversity and establish long-term processes that protect agroecosystem function in community gardens. However, greater recognition of the value of wildness coupled with more allowances for wildness in garden rules could help increase the diversity of ecological habitat and resources that community gardens support.

Conclusion

Community gardens are unique agroecosystems shaped by the practical demands of growing a diversity of crops and ornamental plants in relatively small urban spaces as well as the aesthetic and management preferences of each community gardener. Community gardeners shared several management considerations and aesthetic values, which they prioritized according to their individual needs, motivations, and preferences. While community gardens are not held to the same standards of uniform tidiness that are common among conventional agricultural fields and residential grass lawns, tidy maintenance endures as a socially accepted aesthetic norm in community gardens. Despite formal rules and informal pressures to conform to the tidy aesthetic norm, about half the community gardeners studied here were willing to break with the tidy norm and cultivate garden plots that incorporated wildness. Wild plot gardeners had different reasons for doing so, but most shared an appreciation for wild forms of urban nature potentially associated with their experiences with environmental education of some kind. Tidy garden plots required frequent weeding and trimming of plants arranged in orderly rows, which imply lower plant diversity and structural complexity compared to wild plots that were more tolerant of useful weeds and past-harvest plants. Wild plot gardeners were also willing to use sustainable soil management practices that may not be aesthetically appealing under the tidy aesthetic norm. Based on the characteristics of tidy and wild plot styles, wild garden plots may thus help further diversify the ecological habitat and resources provided by community gardens.

Table 4.1 Summary of focus group and interview participant demographics, garden locations, and garden management aesthetics.

	Focus group	**Interviews**
Age	57-77	30-71
Gender	Female (6) Male (1)	Female (4) Male (3) Nonbinary (1)
Race/ethnicity	White (7)	Asian (2) Latino (3) White (3)
Nationality	USA (7)	El Salvador (1) Mexico (1) Peru (1) USA (5)
Highest education level	Associate (1) Bachelor (3) Master (2) Doctorate (1)	Middle School (1) Bachelor (3) Master (4)
Annual Income	< $30,000 (1) $30,000 - $60,000 (4) > $120,000 (1) Prefer Not to Answer (1)	< $30,000 (1) $30,000 - $60,000 (1) $60,000 - $90,000 (2) $90,000 - $120,000 (2) > $120,000 (1) Prefer Not to Answer (1)
Community Garden Location	Santa Cruz (3) San Jose (4)	Santa Cruz (7) San Jose (1)
Predominant Management Aesthetic	Tidy (4) Wild (3)	Tidy (4) Wild (4)

Figure 4.1 Focus group participant responses to photovoice prompt #1. On the left are photos submitted by each participant with their accompanying captions on the right. Captions appear as the original, exact text submitted by participants.

Prompt #1: What does your ideal garden plot look like?

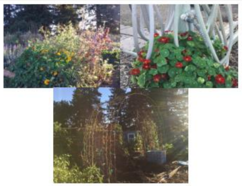
	Pictured are plants in varying degrees of growth maturity consisting of yellow corn, collard greens, kale, garlic, green and bulb onions, beets, radish, cantaloupe, cucumber, bell peppers, zucchini and lots of tomato plants. Not visible in the picture are my potted berries; black, blue and raspberry.
	My ideal garden has a grape arbor for shade to sit and relax on a hot summer's day. It has weed free beds and mulched pathways. There is room for volunteer plants to pop up. Besides growing food for people, my ideal garden supports other life forms, from birds to spiders to microscopic organisms. Worms live happily in a compost pile. The garden is in a public space so others can enjoy looking at it and perhaps be inspired to garden.
	Dog friendly! Attracts Butterflies, and Tomatoes galore!
	My ideal garden is regenerative to absorb carbon emissions. Compost made from food scraps collected by my neighbors is placed over the soil throughout the year. Plants are always growing, with cover crops in the winter. The picture shows tomatoes, chard, asparagus, basil and parsley. Soil health helps reduce water usage.
	My ideal garden, healthy growth of veggies, weed and gopher barrier along with a gate and fence enclosing it. Containers, raised beds and veggies galore.
	My ideal garden plot is a wild mix of flowers, herbs, and vegetables. And it has an artfully rusted arch that's completely green at the height of the season. Volunteer nasturtiums crowd the base of the hose. You can't see them in these photos, but worn bricks and mosaic stepping stones make a winding path through the foliage.
	My ideal garden started with the garden table and chairs, then the path became obvious. I enjoy spending time in the garden writing, painting, drawing, planning, enjoying a cup of tea, taking in the sights and sounds, especially on a day that is misty or foggy. My ideal garden must have flowers to attract the beneficials then planting my favorites; zucchini, tomatoes, cucumbers and all sorts of alliums. Center left and center right photos are allium blooms Top left is the bee balm blooms, then the 15' high Jerusalem artichoke blooms (in the sunflower family) and the lower left, just love the gemstone colors of this lettuce variety.

Figure 4.2 Focus group participant responses to photovoice prompt #2. On the left are photos submitted by each participant with accompanying captions to their right. Captions appear as the original, exact text submitted by participants.

Prompt #2: What does a big challenge in your garden look like?

	I like to plant yellow sweet corn in my garden. And my neighboring gardener plants blue corn. The blue cross pollinates with the sweet corn and renders the yellow unfit for consumption. The blue corn is allowed to dry out and is ground into a flour. Pictured on the left is yellow sweet corn, and on the right is blue corn. Pictured in the middle is the ever so frequent result.
	A big challenge in my garden will be the asparagus bed. It was here when I got the garden. I haven't done a thing with it except a heavy mulch. I also sowed fava beans to add nitrogen to the soil. I'll have to decide if I want to take it up and replant it or use the bed for something else. It only made pencil asparagus last spring. If you look closely you can see a pumpkin that wound its way over there. In the background you can see the garden next to me with the green watering can. Many gardeners are cleaning up their plots from the summer's growth. The photograph was taken on an overcast day when it was trying to rain.
	The biggest challenge in the garden remains the humans, notice our garden shed was just torched by an arsonist, which had all our shared tools, wheelbarrows, hoses, shovels, and pickaxes. They also cut the fence and steal hoses and tools. Humans also dumped seven guinnea pigs into the garden. The other huge challenge is conserving water. Main water was on only three days a week, so saving water is crucial.
	The biggest challenge for my garden is bermudagrass, which surrounds the plot and spreads into the garden by sending out shoots both above and below ground. In addition it produces very hardy seeds which are shown in the picture. Nearly every time I visit the garden I dig out more of this weed, and attempt to cut it down, but it definitely has the upper hand.
	Right: Keeping folks from stealing my flowers and veggies is the greatest challenge to my garden. The fence and gate help with that challenge along with the latch and padlock I installed. This year no theft of anything in the plot yay! Top left: Another shot of the whole outside of the fence with gate. Bottom left: This used to be my community garden for the last 9 years till I moved into the fenced and gated garden just opposite of my old garden.
	Tomato virus. Tomato virus. Tomato virus. I've had persistent trouble with it. I suspect it's also affecting my cucumbers, although I'm not quite sure. My tomato and cucumber harvest has been very limited for the past 3 or 4 years.
	My greatest challenge is the overall time management. Managing the different critters, weeds and plant issues … not sure what is eating the tomatoes, but I hope it is being enjoyed! The snails and slugs always finding places to hide and then enjoying the buffet when I'm away. The mounds of fresh soil turned up by the gophers is obvious in every quadrant letting me know that they are busy underground… I'm pretty good at trapping them … it takes time, patience and skill. The powdery mildew; happy that I have found a working solution from watching many videos online … I am grateful for the challenges and the freedom to figure it out as I go.

Figure 4.3 Focus group participant responses to photovoice prompt #3. On the left are photos submitted by each participant with accompanying captions to their right. Captions appear as the original, exact text submitted by participants.

Prompt #3: What does an instance of either harmony or conflict in your garden look like?

	I have devised a garden routine which prevents the intrusion of weeds into my garden. On every visit to my garden, and before leaving I take a hoe and while walking around my garden I knock down all new growth weeds. I have been doing this for six years now and not surprisingly there has been a near elimination of any emergent weeds.
	Yes, I have gophers, slugs and snails, bindweed, Bermuda grass, everyone's conflict!. But to find some harmony I dug into the compost pile. These are liberated worm bin worms. It's impossible to separate them all when adding the worm compost. There were also spiders making a home in the pile. I bring all the kitchen scraps from home. The pile also has any clippings from the garden. I didn't put in the sweet pea vine because they had some mildew. But now I know how to treat it!
	Planting Zinnias provided harmony in the garden. Pure Beauty for humans, delicious leaves and smells for my dog, and pollen for the beautiful Swallowtail butterflies who visited daily. Pollinators heaven.
	After the rain this past weekend many arugula seedlings appeared which are shown in the picture. They are the result of seeds which fell from a springtime cover of many 3-4 foot plants. This year, in the interest of greater harmony, the plants will be thinned and greens harvested before the cycle of dense tall plants in followed by numerous seedlings in the fall is repeated.
	The first photo illustrates that opossums are alive and well in my garden…they are both beneficial and a challenge. They eat ticks and snails but also love my broccoli, kale, tomatoes and Brussels too. I live catch them and take them elsewhere. Also rats are another challenge whom I also live catch with Have a Heart live trap and take them elsewhere. Second and third photos show the flowers I've landed attracting honey and bumble bees as well as butterflies but haven't been able to capture a photo of those pollinators. Hummers are also attracted to the variety of flowers. I have a bird/ bee bath in the garden to support their lives as well. The fourth photo depicts a mud wasp and so far unsure of benefit nor challenge…well except for the possibility of a sting. I am sure they eat insects.
	It's a little hard to see, but there are two tails sticking out of the pocket of my garden tool bag. When I opened my bag, I heard a rustling sound and that's when I noticed the tails. I thought it might be mice (who seem to like my tool bag) but this time two very large lizards ran out. There's so much wildlife in my garden. I've had some magical moments--I think my favorite was the hummingbird who came along and took a long bath in the hose spray while I was watering seeds, close enough to touch.
	An instance of harmony with weeds for me is the lovely borage plant pop ups with its edible flowers. Especially since the recent rain the new volunteers are numerous. The bees and other beneficials love them and they are all over my garden. It's an easy to grow annual, reseeds itself so acts like a perennial (weed).😊 It is used as a culinary herb and the flowers are popular for salad mixes and to decorate cheeses and chocolates. The color is so intense, love how it ranges from magenta to indigo.

REFERENCES

Achury, R., D. A. Holway, and A. V. Suarez. 2021. Pervasive and persistent effects of ant invasion and fragmentation on native ant assemblages. Ecology 102.

Alberti, M. 2005. The Effects of Urban Patterns on Ecosystem Function. International Regional Science Review 28:168–192.

Alberti, M., J. M. Marzluff, E. Shulenberger, G. Bradley, C. Ryan, and C. Zumbrunnen. 2003. Integrating humans into ecology: Opportunities and challenges for studying urban ecosystems. BioScience 53:143–158.

Altieri, M. A. 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems and Environment 74:19–31.

Altieri, M. A., D. K. Letourneau, J. R. Davis, M. A. Altieri, D. K. Letourneau, and J. R. Davis. 1983. Developing Sustainable Agroecosystems. BioScience 33:45–49.

Amarasekare, P., and R. M. Nisbet. 2001. Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. American Naturalist 158:572–584.

Andow, D. A. 1991. Vegetational Diversity and Arthropod Population Response. Annual Review of Entomology 36.

Andow, D. A., and D. R. Prokrym. 1990. Plant structural complexity and host-finding by a parasitoid. Oecologia 82:162–165.

Andrade, R., J. Franklin, K. L. Larson, C. M. Swan, S. B. Lerman, H. L. Bateman, P. S. Warren, and A. York. 2021. Predicting the assembly of novel communities in urban ecosystems. Landscape Ecology 36:1–15.

Aronson, M. F. J., C. A. Lepczyk, K. L. Evans, M. A. Goddard, S. B. Lerman, J. S. MacIvor, C. H. Nilon, and T. Vargo. 2017. Biodiversity in the city: key challenges for urban green space management. Frontiers in Ecology and the Environment 15:189–196.

Aronson, M. F. J., H. Nilon, Charles, C. A. Lepczyk, T. S. Parker, P. S. Warren, S. S. Cilliers, M. A. Goddard, A. K. Hahs, C. Herzog, M. Katti, F. A. La Sorte, N. S. G. Williams, and W. Zipperer. 2016. Hierarchical filters determine community assembly of urban species pools. Ecology 97:2952–2963.

August, P. V. 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. Ecology 64:1495–1507.

Avissar, R. 1996. Potential effects of vegetation on the urban thermal environment. Atmospheric Environment 30:437–448.

Avolio, M., D. E. Pataki, G. D. Jenerette, S. Pincetl, L. W. Clarke, J. Cavender-Bares, T. W. Gillespie, S. E. Hobbie, K. L. Larson, H. R. McCarthy, and T. L. E. Trammell. 2020. Urban plant diversity in Los Angeles, California: Species and functional type turnover in cultivated landscapes. Plants People Planet 2:144–156.

Badgley, C., T. M. Smiley, R. Terry, E. B. Davis, L. R. G. DeSantis, D. L. Fox, S. S. B. Hopkins, T. Jezkova, M. D. Matocq, N. Matzke, J. L. McGuire, A. Mulch, B. R. Riddle, V. L. Roth, J. X. Samuels, C. A. E. Strömberg, and B. J. Yanites. 2017, March 1. Biodiversity and Topographic Complexity: Modern and Geohistorical Perspectives. Elsevier Ltd.

Banks, J. E. 1998. The scale of landscape fragmentation affects herbivore response to vegetation heterogeneity. Oecologia 117:239–246.

Barraclough, L. R. 2009. South central farmers and shadow hills homeowners: Land use policy and relational racialization in Los Angeles. Professional Geographer 61:164–186.

Barton, K. 2020. MuMIn: Multi-Model Inference. R package version 1.43.17. Version 1:18.

Bascompte, J., and P. Jordano. 2014. Mutualistic networks. Page (S. Levin and H. S. Horn, Eds.). Princeton University Press, Princeton, NJ.

Bassett, T. J. 1981. Reaping on the Margins: A Century of Community Gardening in America. Landscape 25:1–8.

Bates, D. 2007. The lme4 Package.

Beaumelle, L., A. Auriol, M. Grasset, A. Pavy, D. Thiéry, and A. Rusch. 2021. Benefits of increased cover crop diversity for predators and biological pest control depend on the landscape context. Ecological Solutions and Evidence 2.

Beck, T. B., J. E. Heimlich, and M. F. Quigley. 2002. Gardeners' perceptions of the aesthetics, manageability, and sustainability of residential landscapes. Applied Environmental Education and Communication 1:163–172.

Belaire, J. A., L. M. Westphal, and E. S. Minor. 2016. Different social drivers, including perceptions of urban wildlife, explain the ecological resources in residential landscapes. Landscape Ecology 31:401–413.

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.

van den Berg, A. E., and M. van Winsum-Westra. 2010. Manicured, romantic, or wild? The relation between need for structure and preferences for garden styles. Urban Forestry and Urban Greening 9:179–186.

Bersier, L.-F., C. Banasek-Richter, and M.-F. Cattin. 2002. Quantitative Descriptors of Food-Web Matrices. Ecology 83:2394–2407.

Birkhofer, K., A. Fließbach, D. H. Wise, and S. Scheu. 2008. Generalist predators in organically and conventionally managed grass-clover fields: Implications for conservation biological control. Annals of Applied Biology 153:271–280.

Blüthgen, N., and A. M. Klein. 2011. Functional complementarity and specialisation: The role of biodiversity in plant-pollinator interactions. Basic and Applied Ecology 12:282–291.

Borror, D. J., and R. E. White. 1970. A field guide to insects: America north of Mexico. 2nd edition. Houghton Mifflin Harcourt, New York.

Bourdieu, P. 1977. Outline of a Theory of Practice. 16th edition. Cambridge University Press, Cambridge, UK.

Bourdieu, P. 1986. The forms of capital. Pages 241–258 Handbook of Theory and Research for the Sociology of Education. Greenwood Press, Westport, CT.

Braun, V., and V. Clarke. 2012. Thematic Analysis. Pages 57–71 APA Handbook of Research Methods in Psychology. American Psychological Association.

Breuste, J., J. Niemelä, and R. P. H. Snep. 2008. Applying landscape ecological principles in urban environments. Landscape Ecology 23:1139–1142.

Buczkowski, G., and D. S. Richmond. 2012. The effect of urbanization on ant abundance and diversity: A temporal examination of factors affecting biodiversity. PLoS ONE 7.

Burkman, C. E., and M. 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.

Burns, L. 2021. Challenges to Habitus: Scruffy Hedges and Weeds in the Irish Countryside. Sociologia Ruralis 61:2–25.

Burton, R. J. F. 2012. Understanding Farmers’ Aesthetic Preference for Tidy Agricultural Landscapes: A Bourdieusian Perspective. Landscape Research 37:51–71.

Burton, R. J. F., C. Kuczera, and G. Schwarz. 2008. Exploring farmers’ cultural resistance to voluntary agri-environmental schemes. Sociologia Ruralis 48:16–37.

Butler-Bowdon, E. 2001. Lawn and order: Aesthetics and architecture in australian suburbia. Studies in the History of Gardens and Designed Landscapes 21:108–114.

Byrne, D. N. 1999. Migration and dispersal by the sweet potato whitefly, Bemisia tabaci. Page Agricultural and Forest Meteorology.

Cabral, I., J. Keim, R. Engelmann, R. Kraemer, J. Siebert, and A. Bonn. 2017. Ecosystem services of allotment and community gardens: A Leipzig, Germany case study. Urban Forestry and Urban Greening 23:44–53.

Campbell-Arvai, V. 2019. Engaging urban nature: improving our understanding of public perceptions of the role of biodiversity in cities. Urban Ecosystems 22:409–423.

Centre for Land and Biological Resources Research. 1993. Hymenoptera of the World: An identificaiton guide to families. Page (H. Goulet and J. T. Huber, Eds.). Agriculture Canada, Ottawa, Ontario.

Chaplin-Kramer, R., and C. Kremen. 2012. Pest control experiments show benefits of complexity at landscape and local scales. Ecological Applications 22:1936–1948.

Chase, J. M., A. Jeliazkov, E. Ladouceur, and D. S. Viana. 2020. Biodiversity conservation through the lens of metacommunity ecology. Blackwell Publishing Inc.

Clarke, K. M., B. L. Fisher, and G. Lebuhn. 2008. The influence of urban park characteristics on ant (Hymenoptera, Formicidae) communities. Urban Ecosystems 11:317–334.

Colazza, S., A. Fucarino, E. Peri, G. Salerno, E. Conti, and F. Bin. 2004. Insect oviposition induces volatile emission in herbaceous plants that attracts egg parasitoids. Journal of Experimental Biology 207:47–53.

Colding, J., M. Giusti, A. Haga, M. Wallhagen, and S. Barthel. 2020. Enabling relationships with nature in cities. Sustainability (Switzerland) 12.

Cook, R. M., and S. F. Hubbard. 1977. Adaptive Searching Strategies in Insect Parasites. Journal of Animal Ecology 46:115–125.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175–1182.

Dale, A. G., and S. D. Frank. 2018. Urban plants and climate drive unique arthropod interactions with unpredictable consequences. Current Opinion in Insect Science 29:27–33.

Dallas, T. 2014. Metacom: An R package for the analysis of metacommunity structure. Ecography 37:402–405.

Dean, R. L., and J. H. Connell. 1987. Marine invertebrates in an algal succession. III. Mechanisms linking habitat complexity with diversity. Page Mar. Biol. Ecol.

Delgado de la flor, Y. A., K. I. Perry, K. J. Turo, D. M. Parker, J. L. Thompson, and M. M. Gardiner. 2020. Local and landscape-scale environmental filters drive the functional diversity and taxonomic composition of spiders across urban greenspaces. Journal of Applied Ecology 57:1570–1580.

Detrain, C., F. J. Verheggen, L. Diez, B. Wathelet, and E. Haubruge. 2010. Aphid-ant mutualism: How honeydew sugars influence the behaviour of ant scouts. Physiological Entomology 35:168–174.

Dormann, C. F., B. Gruber, and J. Fründ. 2008. Introducing the bipartite Package: Analysing Ecological Networks. R News 8:8–11.

Duffy, J. E. 2002. Biodiversity and ecosystem function: The consumer connection. Oikos 99:201–219.

Dyer, L. A., T. R. Walla, H. F. Greeney, J. O. Stireman, and R. F. Hazen. 2010. Diversity of Interactions: A Metric for Studies of Biodiversity. Biotropica 42:281–289.

Egerer, M. H., C. Arel, M. D. Otoshi, 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., C. Arel, M. D. Otoshi, R. D. Quistberg, P. Bichier, and S. M. Philpott. 2017b. Urban arthropods respond variably to changes in landscape context and spatial scale. Journal of Urban Ecology 3:1–10.

Egerer, M. H., H. Liere, B. B. Lin, S. Jha, P. Bichier, and S. M. Philpott. 2018a. Herbivore regulation in urban agroecosystems: Direct and indirect effects. Basic and Applied Ecology 29:44–54.

Egerer, M. H., S. M. Philpott, P. Bichier, S. Jha, H. Liere, and B. B. Lin. 2018b. Gardener well-being along social and biophysical landscape gradients. Sustainability 10:1–14.

Egerer, M., K. Li, and T. W. Y. Ong. 2018c. Context Matters : Contrasting Ladybird Beetle Responses to Urban sustainability Context Matters : Contrasting Ladybird Beetle Responses to Urban Environments across Two US Regions. Sustainability 10:1–17.

Egerer, M., H. Liere, A. Lucatero, and S. M. Philpott. 2020a. Plant damage in urban agroecosystems varies with local and landscape factors. Ecosphere 11:1–19.

Egerer, M., H. Liere, A. Lucatero, and S. M. Philpott. 2020b. Plant damage in urban agroecosystems varies with local and landscape factors. Ecosphere 11.

Faeth, S. H., C. Bang, and S. Saari. 2011. Urban biodiversity: patterns and mechanisms. Annals of the New York Academy of Sciences 1223:69–81.

Faeth, S. H., W. A. Marussich, E. Shochat, and P. S. Warren. 2005. Trophic Dynamics in Urban Communities. BioScience 55:399.

Fan, Y., L. Mccann, and H. Qin. 2017. Western Agricultural Economics Association Households' Adoption of Drought Tolerant Plants: An Adaptation to Climate Change? Page Source: Journal of Agricultural and Resource Economics.

Fattorini, S., C. Mantoni, L. De Simoni, and Di. M. P. Galassi. 2018, March 1. Island biogeography of insect conservation in urban green spaces. Cambridge University Press.

Favret, C., and G. L. Miller. 2014. AphID. https://aphid.aphidnet.org/.

Fenoglio, M. S., M. R. Rossetti, and M. Videla. 2020. Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. Global

Ecology and Biogeography 29:1412–1429.

Fenoglio, M. S., M. Videla, A. Salvo, and G. Valladares. 2013. Beneficial insects in urban environments: Parasitism rates increase in large and less isolated plant patches via enhanced parasitoid species richness. Biological Conservation 164:82–89.

Fenoglio, M. S., V. Werenkraut, J. M. Morales, and A. Salvo. 2017. A hierarchical multi-scale analysis of the spatial relationship between parasitism and host density in urban habitats. Austral Ecology 42:732–741.

Finke, D. L., and R. F. Denno. 2002. Intraguild Predation Diminished in Complex-Structured Vegetation: Implications for Prey Suppression. Ecology 83:643–652.

Fisher, K. E., P. M. Dixon, G. Han, J. S. Adelman, and S. P. Bradbury. 2021. Locating large insects using automated VHF radio telemetry with a multi-antennae array. Methods in Ecology and Evolution 12:494–506.

Fox, J., G. G.G., H. S., G. R., Monette, H. Nilsson, B. Ripley, S. Weisberg, and M. J. Fox. 2007. Companion to Applied Regression. The car Package. R package.

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.

Galt, R. E., L. C. Gray, and P. Hurley. 2014. Subversive and interstitial food spaces: transforming selves, societies, and society-environment relations through urban agriculture and foraging. Local Environment 19:133–146.

Gardiner, M. M., C. E. Burkman, and S. P. Prajzner. 2013. The value of urban vacant land to support arthropod biodiversity and ecosystem services. Environmental Entomology 42:1123–1136.

Geervliet, J. B. F., S. Ariëns, M. Dicke, and L. E. M. Vet. 1998. Long-distance assessment of patch profitability through volatile infochemicals by the parasitoids Cotesia glomerata and C. rubecula (Hymenoptera: Braconidae). Biological Control 11:113–121.

Geslin, B., B. Gauzens, E. Thebault, and I. Dajoz. 2013. Plant Pollinator Networks along a Gradient of Urbanisation. PLoS ONE 8:1–13.

Gingras, D., P. Dutilleul, and G. Boivin. 2003. Effect of plant structure on host finding capacity of lepidopterous pests of crucifers by two Trichogramma parasitoids. Biological Control 27:25–31.

Girling, R. D., A. Stewart-Jones, J. Dherbecourt, J. T. Staley, D. J. Wright, and G. M. Poppy. 2011. Parasitoids select plants more heavily infested with their caterpillar hosts: A new approach to aid interpretation of plant headspace volatiles. Proceedings of the Royal Society B: Biological Sciences 278:2646–2653.

Glennie, C. 2020. Cultivating Place: Urban Development and the Institutionalization of Seattle's P-Patch Community Gardens. City and Community 19:726–746.

Goddard, M. A., A. J. Dougill, and T. G. Benton. 2013. Why garden for wildlife? Social and ecological drivers, Motivations and barriers for biodiversity management in residential landscapes. Ecological Economics 86:258–273.

Gómez-Navarro, C., D. E. Pataki, E. R. Pardyjak, and D. R. Bowling. 2021. Effects of vegetation on the spatial and temporal variation of microclimate in the urbanized Salt Lake Valley. Agricultural and Forest Meteorology 296.

González-Chang, M., S. Tiwari, S. Sharma, and S. D. Wratten. 2019. Habitat Management for Pest Management: Limitations and Prospects. Annals of the Entomological Society of America 112:302–317.

Grevstad, F. S., and B. W. Klepetka. 1992. The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. Oecologia 92:399–404.

Griffith, G. E., J. M. Omernik, D. W. Smith, T. D. Cook, E. Tallyn, K. Moseley, and C. B. Johnson. 2016. Ecoregions of California. Page US Geological Open-File Report 2016–1021.

Grover, C. D., K. C. Dayton, S. B. Menke, and D. A. Holway. 2008. Effects of aphids on foliar foraging by Argentine ants and the resulting effects on other arthropods. Ecological Entomology 33:101–106.

Gurr, G. M., S. D. Wratten, D. A. Landis, and M. You. 2017, January 31. Habitat Management to Suppress Pest Populations: Progress and Prospects. Annual Reviews Inc.

Hajian-Forooshani, Z., L. Schmitt, N. Medina, and J. Vandermeer. 2019. Trophic-specific responses to migration in empirical metacommunities. Oikos 00:1–7.

Hanski, I. 1998. Metapopulation dynamics. Nature 396:9.

Hartig, F. 2021. Package ' DHARMa .'

He, H., L. Liu, S. Munir, N. H. Bashir, Y. Wang, J. Yang, and C. Li. 2019, September 1. Crop diversity and pest management in sustainable agriculture. Chinese Academy of Agricultural Sciences.

Hodge, M. A. 1999. The Implications of Intraguild Predation for the Role of Spiders in Biological Control. Page Source: The Journal of Arachnology.

Holway, D. A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive argentine ant. Ecology 80:238–251.

Hope, D., C. Gries, W. Zhu, W. F. Fagan, C. L. Redman, N. B. Grimm, A. L. Nelson, C. Martin, and A. Kinzig. 2003. Socioeconomics drive urban plant diversity. PNAS 100:8788–8792.

Hu, X., M. F. Lima, R. McLean, and Z. Sun. 2022. Exploring preferences for biodiversity and wild parks in Chinese cities: A conjoint analysis study in Hangzhou. Urban Forestry and Urban Greening 73.

Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27:343–383.

Human, D. M., and K. G. Gordon. 1996. Exploitation and interference competition between the invasive Argentine ant, I.inepithema humile, and native ant species. Page Oecologia. Springer-Verlag.

Hwang, Y. H., Z. E. J. Yue, S. K. Ling, and H. H. V. Tan. 2019. It's ok to be wilder: Preference for natural growth in urban green spaces in a tropical city. Urban Forestry and Urban Greening 38:165–176.

Inbar, M., and D. Gerling. 2008. Plant-mediated interactions between whiteflies, herbivores, and natural enemies. Annual Review of Entomology 53:431–448.

Iowa State University Department of Entomology. 2003. BugGuide. https://bugguide.net/.

Irvin, N. A., J. R. Hagler, and M. S. Hoddle. 2018. Measuring natural enemy dispersal from cover crops in a California vineyard. Biological Control 126:15–25.

Ives, A. R., B. J. Cardinale, and W. E. Snyder. 2005. A synthesis of subdisciplines: Predator-prey interactions, and biodiversity and ecosystem functioning. Ecology Letters 8:102–116.

Kareiva, P., and R. Perry. 1989. Leaf overlap and the ability of ladybird beetles to search among plants. Ecological Entomology 14:127–129.

Keeler, B. L., P. Hamel, T. McPhearson, M. H. Hamann, M. L. Donahue, K. A. Meza Prado, K. K. Arkema, G. N. Bratman, K. A. Brauman, J. C. Finlay, A. D. Guerry, S. E. Hobbie, J. A. Johnson, G. K. MacDonald, R. I. McDonald, N. Neverisky, and S. A. Wood. 2019, January 1. Social-ecological and technological factors moderate the value of urban nature. Nature Publishing Group.

Keitt, T. H., D. L. Urban, and B. T. Milne. 1997. Detecting Critical Scales in Fragmented Landscapes. Conservation Ecology 1:1–18.

Kim, M. S., S. H. Ahn, I. J. Jeong, and T. K. Lee. 2021. Water quality drives the regional patterns of an algal metacommunity in interconnected lakes. Scientific reports 11:13601.

Kovalenko, K. E., S. M. Thomaz, and D. M. Warfe. 2012. Habitat complexity: Approaches and future directions. Hydrobiologia 685:1–17.

Kral-O’Brien, K. C., and J. P. Harmon. 2021, June 1. The expanding role of movement behavior in insect conservation ecology. Elsevier Inc.

Kring, J. B. 1972. Flight Behavior of Aphids. Annual Review of Entomology 17:461–492.

Kruess, A., and T. Tscharntke. 1994. Habitat Fragmentation, Species Loss, and Biological Control. Science 264:1581–1584.

de la Sancha, N. U., C. L. Higgins, S. J. Presley, and R. E. Strauss. 2014. Metacommunity structure in a highly fragmented forest: Has deforestation in the Atlantic Forest altered historic biogeographic patterns? Diversity and Distributions 20:1058–1070.

Laage-Thomsen, J., and A. Blok. 2021. Varieties of green: On aesthetic contestations over urban sustainability pathways in a Copenhagen community garden. Environment and Planning E: Nature and Space 4:275–295.

Laliberté, E., and J. M. Tylianakis. 2010. Deforestation homogenizes tropical parasitoid — host networks. Ecology 91:1740–1747.

Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve nataural 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.

Lassau, S. A., and D. F. Hochuli. 2004. Effects of habitat complexity on ant assemblages. Ecography 27:157–164.

Lassau, S. A., D. F. Hochuli, G. Cassis, and C. A. M. Reid. 2005. Effects of habitat complexity on forest beetle diversity: Do functional groups respond consistently? Diversity and Distributions 11:73–82.

Lawton, J. H. 1983. Plant Architecture and the Diversity of Phytophagous Insects:23–39.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters 7:601–613.

Leibold, M. A., and G. M. Mikkelson. 2002. Coherence, species turnover, and boundary clumping: Elements of meta-community structure. Oikos 97:237–250.

Letourneau, D. K., I. Ambrecht, B. S. Rivera, J. M. Lerma, E. J. Carmona, M. C. Daza, S. Escobar, V. Galindo, C. Gutiérrez, S. D. López, J. L. Mejía, A. M. A. Rangel, J. H. Rangel, L. Rivera, C. A. Saavedera, A. M. Torres, and A. R. Trujillo. 2011. Does plant diversity benefit agroecosystems? A synthetic review. Ecological Applications 21:9–21.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. American Entomologist 15:237–240.

Li, J., and J. I. Nassauer. 2020, September 1. Cues to care: A systematic analytical review. Elsevier B.V.

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 5:1–12.

Liere, H., M. Egerer, C. Sanchez, P. Bichier, and S. M. Philpott. 2020. Social Context Influence on Urban Gardener Perceptions of Pests and Management Practices. Frontiers in Sustainable Food Systems 4:1–14.

Lin, B. B., M. H. Egerer, and A. Ossola. 2018. Urban gardens as a space to engender biophilia: Evidence and ways forward. Frontiers in Built Environment 4:1–10.

Lin, B. B., and R. A. Fuller. 2013. Sharing or sparing? How should we grow the world's cities? Journal of Applied Ecology 50:1161–1168.

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.

Lindemann-Matthies, P., and H. Brieger. 2016. Does urban gardening increase aesthetic quality of urban areas? A case study from Germany. Urban Forestry and Urban Greening 17:33–41.

Lindemann-Matthies, P., and T. Marty. 2013. Does ecological gardening increase species richness and aesthetic quality of a garden? Biological Conservation 159:37–44.

Loke, L. H. L., and R. A. Chisholm. 2022. Measuring habitat complexity and spatial heterogeneity in ecology. Ecology Letters 25:2269–2288.

Lowe, E. C., C. G. Threlfall, S. M. Wilder, D. F. Hochuli, and E. C. Lowe Lowe. 2018. Environmental drivers of spider community composition at multiple scales along an urban gradient. Biodivers Conserv 27:829–852.

Lowenstein, D. M., and E. S. Minor. 2018. Herbivores and natural enemies of brassica crops in urban agriculture. Urban Ecosystems 21:519–529.

Ludwig, M., H. Schlinkert, and R. Meyhöfer. 2018. Wind-modulated landscape effects on colonization of Brussels sprouts by insect pests and their syrphid antagonists. Agricultural and Forest Entomology 20:141–149.

MacArthur, R. H. 1965. Patterns of species diversity. Biological Reviews 40:510–533.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press.

Macfadyen, S., P. G. Craze, A. Polaszek, K. van Achterberg, and J. Memmott. 2011. Parasitoid diversity reduces the variability in pest control services across time on farms. Proceedings of the Royal Society B: Biological Sciences 278:3387–3394.

MacFadyen, S., R. Gibson, A. Polaszek, R. J. Morris, P. G. Craze, R. Planqué, W. O. C. Symondson, and J. Memmott. 2009. Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? Ecology Letters 12:229–238.

Mares, T., and D. G. Peña. 2010. Urban agriculture in the making of insurgent spaces in Los Angeles and Seattle. Pages 241–254 Insurgent Public Space: Guerrilla Urbanism and the Remaking of Contemporary Cities.

Marquis, R. J., N. B. Road, and S. Louis. 1996. Plant Morphology and Recruitment of the Third Trophic Level: Subtle and Little- Recognized Defenses? Oikos 75:330–334.

Marrec, R., O. Pontbriand-Pare, S. Legault, and P. M. A. James. 2018. Spatiotemporal variation in drivers of parasitoid metacommunity structure in continuous forest landscapes. Ecosphere 9.

Marshall, S. A. 2006. Insects: Their Natural History and Diversity: With a Photographic Guide to Insects of Eastern North America. 2nd edition. Firefly Books, Buffalo, NY.

Mata, L., C. G. Threlfall, N. S. G. Williams, A. K. Hahs, M. Malipatil, N. E. Stork, and S. J. Livesley. 2017. Conserving herbivorous and predatory insects in urban green spaces. Scientific Reports 7:1–12.

Maurer, M. 2021. Chickens, weeds, and the production of green middle-class identity through urban agriculture in deindustrial Michigan, USA. Agriculture and Human Values 38:467–479.

McClintock, N. 2010. Why farm the city? Theorizing urban agriculture through a lens of metabolic rift. Cambridge Journal of Regions, Economy and Society 3:191–207.

McIntyre, N. E. 2000. Ecology of Urban Arthropods: A Review and a Call to Action. Annals of the Entomological Society of America 93:825–835.

McIntyre, N. E., J. Rango, W. F. Fagan, and S. H. Faeth. 2001. Ground arthropod community structure in a heterogeneous urban environment. Landscape and Urban Planning 52:257–274.

McKinney, M. L. 2008. Effects of urbanization on species richness: A review of plants and animals. Urban Ecosystems 11:161–176.

Meehan, T. D., B. P. Werling, D. A. Landis, and C. Gratton. 2011. Agricultural landscape simplification and insecticide use in the Midwestern United States. Proceedings of the National Academy of Sciences of the United States of America 108:11500–11505.

Meineke, E. K., R. R. Dunn, J. O. Sexton, and S. D. Frank. 2013. Urban Warming

Drives Insect Pest Abundance on Street Trees. PLoS ONE 8:2–8.

Meineke, E. K., A. J. Holmquist, G. M. Wimp, and S. D. Frank. 2017. Changes in spider community composition are associated with urban temperature, not herbivore abundance. Journal of Urban Ecology 3.

Meiners, T., and E. Obermaier. 2004. Hide and seek on two spatial scales - Vegetation structure effects herbivore oviposition and egg parasitism. Basic and Applied Ecology 5:87–94.

Menalled, F. D., P. C. Marino, S. H. Gage, and D. A. Landis. 1999. Does agricultural landscape structure affect parasitism and parasitoid diversity? Ecological Applications 9:634–641.

Menke, S. B., R. N. Fisher, W. Jetz, and D. A. Holway. 2007. Biotic and abiotic controls of argentine ant invasion success at local and landscape scales. Ecology 88:3164–3173.

Menke, S. B., and D. A. Holway. 2006. Abiotic factors control invasion by Argentine ants at the community scale. Journal of Animal Ecology 75:368–376.

Mihaljevic, J. R. 2012. Linking metacommunity theory and symbiont evolutionary ecology. Trends in Ecology and Evolution 27:323–329.

Mihaljevic, J. R., B. Joseph, Maxwell, and P. T. J. Johnson. 2015. Using multispecies occupancy models to improve the characterization and understanding of metacommunity structure. Ecology 96:1783–1792.

Miles, L. S., S. T. Breitbart, H. H. Wagner, and M. T. J. Johnson. 2019. Urbanization shapes the ecology and evolution of plant-arthropod herbivore interactions. Frontiers in Ecology and Evolution 7:1–14.

Montefrio, M. J. F., X. R. Lee, and E. Lim. 2020. Aesthetic politics and community gardens in Singapore. Urban Geography:1–21.

Moreira, X., L. Abdala-Roberts, S. Rasmann, B. Castagneyrol, and K. A. Mooney. 2016. Plant diversity effects on insect herbivores and their natural enemies: current thinking, recent findings, and future directions. Current Opinionin Insect Science 14:1–7.

Murdoch, W. W., and A. Stewart-Oaten. 1989. Aggregation by Parasitoids and Predators: Effects on Equilibrium and Stability. The American Naturalist 134:288–310.

Nassauer, J. I. 1988. The Aesthetics of Horticulture: Neatness as a Form of Care.

Horticultural Science 23:973–977.

Nathan, R. 2001. The challenges of studying dispersal. Trends in Ecology and Evolution 16:481–482.

Naumann, I. D. 1991. Hymenoptera. Pages 916–1001 *in* I. D. Naumann, P. B. Carne, J. F. Lawrence, E. S. Nielsen, J. P. Spradberry, R. W. Taylor, M. J. Whitten, and M. J. Littlejohn, editors. The insects of Australia: A textbook for students and research workers. Second. Melbourne University Press, Carlton, Victoria.

Nelson, A. E., and A. A. Forbes. 2014. Urban land use decouples plant-herbivore-parasitoid interactions at multiple spatial scales. PLoS ONE 9.

Nicholson, C. C., and N. M. Williams. 2021. Cropland heterogeneity drives frequency and intensity of pesticide use. Environmental Research Letters 16.

Niemelä, J. 1999. Is there a need for a theory of urban ecology? Urban Ecosystems 3:57–65.

Nighswander, G. P., J. S. Sinclair, A. G. Dale, J. Qiu, and B. V. Iannone. 2021. Importance of plant diversity and structure for urban garden pest resistance. Landscape and Urban Planning 215.

Nooten, S. S., P. Schultheiss, R. C. Rowe, S. L. Facey, and J. M. Cook. 2019. Habitat complexity affects functional traits and diversity of ant assemblages in urban green spaces (Hymeno ptera: Formicidae). Myrmecological News 29:67–77.

Norton, B. A., L. J. Thomson, N. S. G. Williams, and M. J. McDonnell. 2014. The effect of urban ground covers on arthropods: An experiment. Urban Ecosystems 17:77–99.

Oberholtzer, L., C. Dimitri, and A. A. Pressman. 2014. Urban agriculture in the United States: Characteristics, challenges, and technical assistance needs. Journal of Extension 52:#6FEA1.

Obermaier, E., A. Heisswolf, J. Poethke, B. Randlkofer, and T. Meiners. 2008. Plant architecture and vegetation structure: Two ways for insect herbivores to escape parasitism. European Journal of Entomology 105:233–240.

Ofstehage, A. 2022. Tidy Fields and Clean Shirts: A Comparative Ethnography of Good Farming in South Dakota and Luis Eduardo Magalhães. Culture, Agriculture, Food and Environment 44:63–75.

Oksanen, A. J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. Mcglinn, P. R. Minchin, R. B. O. Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and E.

Szoecs. 2020. Package ‘ vegan .’

Ong, T. W., K. Li, A. Lucatero, D. Pak, and L. O. Hawkes. 2020. Taylor Made Landscapes : Using Taylor’s Law to Scale Between Metapopulations and Source-Sinks in Urban Garden Space. Frontiers in Sustainable Food Systems 4:1–13.

Ong, T. W., and J. H. Vandermeer. 2014. Antagonism between two natural enemies improves biological control of a coffee pest: The importance of dominance hierarchies. Biological Control 76:107–113.

Ong, T. W. Y., and W. Liao. 2020. Agroecological Transitions: A Mathematical Perspective on a Transdisciplinary Problem. Frontiers in Sustainable Food Systems 4:1–25.

Ossola, A., M. A. Nash, F. J. Christie, A. K. Hahs, and S. J. Livesley. 2015. Urban habitat complexity affects species richness but not environmental filtering of morphologically-diverse ants. PeerJ 2015.

Otoshi, M. D., 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.

van Oudenhove, L., L. Mailleret, and X. Fauvergue. 2017. Infochemical use and dietary specialization in parasitoids: a meta-analysis. Ecology and Evolution 7:4804–4811.

Parsons, S. E., and S. D. Frank. 2019. Urban tree pests and natural enemies respond to habitat at different spatial scales. Journal of Urban Ecology 5:1–15.

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.

Pereira-Peixoto, M. H., G. Pufal, M. Staab, C. Feitosa Martins, and A. M. Klein. 2016. Diversity and specificity of host-natural enemy interactions in an urban-rural interface. Ecological Entomology 41:241–252.

Perfecto, I., and S. M. Philpott. 2023. Ants (Hymenoptera: Formicidae) and ecosystem functions and services in urban areas: a reflection on a diverse literature. Myrmecol. News 33:103–122.

Philpott, S. M., and P. Bichier. 2017. Local and landscape drivers of predation services in urban gardens. Ecological Applications 27:966–976.

Philpott, S. M., M. H. Egerer, P. Bichier, H. Cohen, R. Cohen, H. Liere, S. Jha, and B. B. Lin. 2020a. Gardener demographics, experience, and motivations drive differences in plant species richness and composition in urban gardens. Ecology and Society 25:1–27.

Philpott, S. M., A. Lucatero, P. Bichier, M. H. Egerer, S. Jha, B. Lin, and H. Liere. 2020b. Natural enemy–herbivore networks along local management and landscape gradients in urban agroecosystems. Ecological Applications 0:1–13.

Philpott, S. M., I. Perfecto, J. Vandermeer, and S. Uno. 2009. Spatial scale and density dependence in a host parasitoid system: An arboreal ant, azteca instabilis, and its pseudacteon phorid parasitoid. Environmental Entomology 38:790–796.

Pianka, E. R. 1966. Convexity, Desert Lizards, and Spatial Heterogeneity. Ecology 47:1055–1059.

St. Pierre, J. I., and K. E. Kovalenko. 2014. Effect of habitat complexity attributes on species richness. Ecosphere 5.

Poisot, T., N. Mouquet, and D. Gravel. 2013. Trophic complementarity drives the biodiversity-ecosystem functioning relationship in food webs. Ecology Letters 16:853–861.

Presley, S. J., C. L. Higgins, C. López-González, and R. D. Stevens. 2009. Elements of metacommunity structure of Paraguayan bats: Multiple gradients require analysis of multiple ordination axes. Oecologia 160:781–793.

Presley, S. J., C. L. Higgins, and M. R. Willig. 2010. A comprehensive framework for the evaluation of metacommunity structure. Oikos 119:908–917.

Price, P. W., C. E. Bouton, P. Gross, B. A, J. N. Thompson, and A. E. Weis. 1980. Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. Most 11:41–65.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

R Development Core Team. 2021. R: A language and environment for statistical computing. Vienna, Austria.

Randlkofer, B., E. Obermaier, J. Casas, and T. Meiners. 2010a. Connectivity counts: Disentangling effects of vegetation structure elements on the searching movement of a parasitoid. Ecological Entomology 35:446–455.

Randlkofer, B., E. Obermaier, M. Hilker, and T. Meiners. 2010b. Vegetation complexity — The influence of plant species diversity and plant structures on plant chemical complexity and arthropods. Basic and Applied Ecology 11:383–395.

Raupp, M. J., P. M. Shrewsbury, and D. A. Herms. 2009. Ecology of Herbivorous Arthropods in Urban Landscapes. Annual Review of Entomology 55:19–38.

Raupp, M. J., P. M. Shrewsbury, J. J. Holmes, and J. A. Davidson. 2001. Plant species diversity and abundance affects the number of arthropod pests in residential landscapes. Journal of Arboriculture 27:222–229.

Rebek, E. J., C. S. Sadof, and L. M. Hanks. 2005. Manipulating the abundance of natural enemies in ornamental landscapes with floral resource plants. Biological Control 33:203–216.

Redlich, S., E. A. Martin, and I. Steffan-Dewenter. 2018. Landscape-level crop diversity benefits biological pest control. Journal of Applied Ecology 55:2419–2428.

Riley, M. 2016. Still Being the “Good Farmer”: (Non-)retirement and the Preservation of Farming Identities in Older Age. Sociologia Ruralis 56:96–115.

Robbins, P. 2012. Lawn people: How grasses, weeds, and chemicals make us who we are. Temple University Press, Philadelphia.

Robbins, P., A. Polderman, and T. Birkenholtz. 2001. Lawns and toxins-an ecology of the city. Cities 18:369–380.

Robbins, P., and J. T. Sharp. 2003. Producing and Consuming Chemicals: The Moral Economy of the American Lawn. Economic Geography 79:425–451.

Rodríguez, M. Á., and B. A. Hawkins. 2000. Diversity, function and stability in parasitoid communities. Ecology Letters 3:35–40.

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.

Rotz, S. 2017. ‘They took our beads, it was a fair trade, get over it’: Settler colonial logics, racial hierarchies and material dominance in Canadian agriculture. Geoforum 82:158–169.

Rowles, A. D., and D. J. O’Dowd. 2007. Interference competition by Argentine ants displaces native ants: Implications for biotic resistance to invasion. Biological Invasions 9:73–85.

Russell, E. P. 1989. Enemies Hypothesis : A Review of the Effect of Vegetational Diversity on Predatory Insects and Parasitoids Diversity on Predatory Insects and Parasitoids. Environmental Entomology 18:590–599.

Saldivar-Tanaka, L., and M. E. Krasny. 2004. Culturing community development, neighborhood open space, and civic agriculture: The case of Latino community gardens in New York City. Agriculture and Human Values 21:399–412.

Samu, F., A. Horváth, D. Neidert, E. Botos, and É. Szita. 2018. Metacommunities of spiders in grassland habitat fragments of an agricultural landscape. Basic and Applied Ecology 31:92–103.

San Jose Parks Recreation & Neighborhood Services. 2022. 2023 Community Gardens Rules and Regulations. San Jose.

Sanford, M. P., P. N. Manley, and D. D. Murphy. 2009. Effects of urban development on ant communities: Implications for ecosystem services and management. Conservation Biology 23:131–141.

Santolamazza-Carbone, S., P. Velasco, P. Soengas, and M. E. Cartea. 2014. Bottom-up and top-down herbivore regulation mediated by glucosinolates in Brassica oleracea var. acephala. Oecologia 174:893–907.

Saqib, H. S. A., P. Liang, M. You, and G. M. Gurr. 2021. Molecular gut content analysis indicates the inter- and intra-guild predation patterns of spiders in conventionally managed vegetable fields. Ecology and Evolution 11:9543–9552.

Saunders, F. P. 2016. Complex Shades of Green: Gradually Changing Notions of the ‘Good Farmer’ in a Swedish Context. Sociologia Ruralis 56:391–407.

Schlinkert, H., C. Westphal, Y. Clough, Z. László, M. Ludwig, and T. Tscharntke. 2015. Plant size as determinant of species richness of herbivores, natural enemies and pollinators across 21 brassicaceae species. PLoS ONE 10:1–18.

Schmidt, M. H., A. Lauer, T. Purtauf, C. Thies, M. Schaefer, and T. Tscharntke. 2003. Relative importance of predators and parasitoids for cereal aphid control. Proceedings of the Royal Society B: Biological Sciences 270:1905–1909.

Schmitz, O. J. 2007. Predator Diversity and Trophic Interactions. Ecology 88:2415–2426.

Shochat, E., P. S. Warren, S. H. Faeth, N. E. McIntyre, and D. Hope. 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology and Evolution 21:186–191.

Shrewsbury, P. M., and M. J. Raupp. 2006. Do top-down or bottom-up forces determine Stephanitis pyrioides abundance in urban landscapes? Ecological Applications 16:262–272.

Sisser, J. M., K. C. Nelson, K. L. Larson, L. A. Ogden, C. Polsky, and R. R. Chowdhury. 2016. Lawn enforcement: How municipal policies and neighborhood norms influence homeowner residential landscape management. Landscape and Urban Planning 150:16–25.

Stahlschmidt, Z. R., and D. Johnson. 2018. Moving targets: determinants of nutritional preferences and habitat use in an urban ant community. Urban Ecosystems 21:1151–1158.

Suarez, A. V., D. T. Bolger, and T. J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology 79:2041–2056.

Sutherland, L. A., and I. Darnhofer. 2012. Of organic farmers and “good farmers”: Changing habitus in rural England. Journal of Rural Studies 28:232–240.

Sutton-Brown, C. A. 2014. Photovoice: A Methodological Guide. Photography and Culture 7:169–185.

Suzuki, Y., and E. P. Economo. 2021. From species sorting to mass effects: spatial network structure mediates the shift between metacommunity archetypes. Ecography 44:715–726.

Taylor, J. R., S. T. Lovell, S. E. Wortman, and M. Chan. 2017. Ecosystem services and tradeoffs in the home food gardens of African American, Chinese-origin and Mexican-origin households in Chicago, IL. Renewable Agriculture and Food Systems 32:69–86.

Tentelier, C., and X. Fauvergue. 2007. Herbivore-induced plant volatiles as cues for habitat assessment by a foraging parasitoid. Journal of Animal Ecology 76:1–8.

Thebault, E., and C. Fontaine. 2010. Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. Science 329:853–856.

Thompson, K., K. C. Austin, R. M. Smith, P. H. Warren, P. G. Angold, and K. J.

Gaston. 2003. Urban domestic gardens (I): Putting small-scale plant diversity in context. Journal of Vegetation Science 14:71–78.

Thomson, L. J., and A. A. Hoffmann. 2010. Natural enemy responses and pest control: Importance of local vegetation. Biological Control 52:160–166.

Tscharntke, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batáry, J. Bengtsson, Y. Clough, T. O. Crist, C. F. Dormann, R. M. Ewers, J. Fründ, R. D. Holt, A. Holzschuh, A. M. Klein, D. Kleijn, C. Kremen, D. A. Landis, W. Laurance, D. Lindenmayer, C. Scherber, N. Sodhi, I. Steffan-Dewenter, C. Thies, W. H. van der Putten, and C. Westphal. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews 87:661–685.

Turlings, T. C. J., J. H. Tumlinson, and W. J. Lewis. 1990. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Science 250:1251–1253.

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. Laliberté, 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. Annu. Rev. Ecol. Evol. Syst 48:25–48.

Tylianakis, J. M., T. Tscharntke, and A. M. Klein. 2006. Diversity, ecosystem function, and stability of parasitoid-host interactions across a tropical habitat gradient. Ecology 87:3047–3057.

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.

Uetz, G. W. 1979. The Influence of Variation in Litter Habitats on Spider Communities. Oecologia (Berl.) 40:29–42.

Uiterwaal, S. F., A. J. Squires, B. A. Grappone, B. Dillard, A. Castaneda, S. L. Kim, and J. P. DeLong. 2023. Intraguild predation is increased in areas of low prey diversity in a generalist predator community. Journal of Animal Ecology.

University of California Agriculture and Natural Resources. 2018. How to Manage Pests: Cole Crops. http://ipm.ucanr.edu/PMG/selectnewpest.cole-crops.html.

Uno, S., J. Cotton, and S. M. Philpott. 2010. Diversity, abundance, and species composition of ants in urban green spaces. Urban Ecosystems 13:425–441.

Vandermeer, J., and R. Carvajal. 2001. Metapopulation Dynamics and the Quality of the Matrix. The American Naturalist 158:211–220.

Vandermeer, J., I. Perfecto, and S. Philpott. 2010. Ecological Complexity and Pest Control in Organic Coffee Production: Uncovering an Autonomous Ecosystem Service. BioScience 60:527–537.

Vergnes, A., I. Le Viol, and P. Clergeau. 2012. Green corridors in urban landscapes affect the arthropod communities of domestic gardens. Biological Conservation 145:171–178.

Vonshak, M., and D. M. Gordon. 2015. Intermediate disturbance promotes invasive ant abundance. Biological Conservation 186:359–367.

Walde, S. J., and W. W. Murdoch. 1988. Spatial density dependence in parasitoids. Annual review of entomology. Vol. 33:441–466.

Wang, C., and M. A. Burris. 1997. Photovoice: Concept, Methodology, and Use for Participatory Needs Assessment. Health Education and Behavior 24:369–387.

Wezel, A., M. Casagrande, F. Celette, J. F. Vian, A. Ferrer, and J. Peigné. 2014. Agroecological practices for sustainable agriculture. A review. EDP Sciences.

Wilby, A., S. C. Villareal, L. P. Lan, K. L. Heong, and M. B. Thomas. 2005. Functional benefits of predator species diversity depend on prey identity. Ecological Entomology 30:497–501.

Williams-Subiza, E. A., C. Brand, and M. L. Miserendino. 2020. Metacommunity structure analysis reveals nested patterns in deconstructed macroinvertebrates assemblages. Ecological Entomology 45:1284–1295.

Williams, B. 2020. “The Fabric of Our Lives”?: Cotton, Pesticides, and Agrarian Racial Regimes in the U.S. South. Annals of the American Association of Geographers 111:422–439.

Winkler, K., F. L. Wäckers, A. J. Termorshuizen, and J. C. van Lenteren. 2010. Assessing risks and benefits of floral supplements in conservation biological control. BioControl 55:719–727.

Wright, D. H., B. D. Patterson, G. M. Mikkelson, A. Cutler, and W. Atmar. 1998. A comparative analysis of nested subset patterns of species composition. Oecologia 113:1–20.

Zhao, J., G. Ayers, E. Grafius, and F. Stehr. 1992. Effects of neighboring nectar-producing plants on populations of pest Lepidoptera and their parasitoids in broccoli plantings. The Great Lakes Entomologist 25:253–258.

Zheng, B., Y. Zhang, and J. Chen. 2011. Preference to home landscape: Wildness or neatness? Landscape and Urban Planning 99:1–8.