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Local and landscape drivers of predation services in urban gardens

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Abstract. In agroecosystems, local and landscape features, as well as natural enemy abundance and richness, are significant predictors of predation services that may result in biological control of pests. Despite the increasing importance of urban gardening for provisioning of food to urban populations, most urban gardeners suffer from high pest problems, and have little knowledge about how to manage their plots to increase biological control services. We examined the influence of local, garden scale (i.e., herbaceous and arboreal vegetation abundance and diversity, ground cover) and landscape (i.e., landscape diversity and surrounding land use types) characteristics on predation services provided by naturally occurring predators in 19 urban gardens in the California central coast. We introduced sentinel pests (moth eggs and larvae and pea aphids) onto greenhouse-raised plants taken to gardens and assigned to open or bagged (predator enclosure) treatments. We found high predation rates with between 40% and 90% of prey items removed in open treatments. Predation services varied with local and landscape factors, but significant predictors differed by prey species. Predation of eggs and aphids increased with vegetation complexity in gardens, but larvae predation declined with vegetation complexity. Smaller gardens experienced higher predation services, likely due to increases in predator abundance in smaller gardens. Several ground cover features influenced predation services. In contrast to patterns in rural agricultural landscapes, predation on aphids declined with increases in landscape diversity. In sum, we report the relationships between several local management factors, as well as landscape surroundings, and implications for garden management.

Key words: *agroecosystem; ants; biological control; lady beetles; spiders; trophic interactions.*

INTRODUCTION

Both local and landscape-level agricultural intensification strongly negatively affect biodiversity and dramatically alter ecosystem services, such as predation services or biological pest control (Tscharntke et al. 2005). Beneficial insects like predators, parasitoids, and pollinators, are worth more than \$57 billion per year in enhanced crop production and improved plant ecosystem function (Losey and Vaughan 2006). Pest control services provided by arthropod predators and parasitoids reduce herbivore populations and plant damage (Settle et al. 1996, Chang and Snyder 2004, Philpott and Armbrrecht 2006) and both vegetation complexity and landscape heterogeneity affect predator and prey communities (Bolger et al. 2000, Shrewsbury and Raupp 2000, Gibb and Hochuli 2002, Uno et al. 2010, Batary et al. 2011, Philpott et al. 2014). Local habitat diversity and complexity (e.g., richness of crop and non-crop plants) affect natural enemy and herbivore communities (Andow 1991, Steffan-Dewenter et al. 2002, Langellotto and Denno 2004, Roschewitz et al. 2005, Schmidt et al. 2005), pest control services (Gardiner et al. 2009), crop damage (Thies and Tscharntke 1999, Den Belder et al. 2002, Thies et al. 2003), and crop yield (Losey and Vaughan 2006, Ricketts

et al. 2008, Liere et al. 2015). The strength of the effect of local habitat enhancements on insect biodiversity, however, is contingent on surrounding landscape quality (e.g., Tscharntke et al. 2005). For example, agricultural fields within diverse landscapes support higher local densities and diversity of arthropods than simplified landscapes, even in fields with low local vegetation diversity (Tscharntke et al. 2005, Bianchi et al. 2006, Chaplin-Kramer et al. 2011). Most knowledge of local and landscape drivers of ecosystem services, such as predation services, is generated in rural landscapes managed at relatively large spatial scales. While the relative importance of landscape context in urban areas is less known, some evidence suggests that the degree to which improvements to local resources increase beneficial insects depends on the amount of impervious cover in a surrounding urban landscape (Bennett and Gratton 2012). For efficient natural pest control, natural enemies must show a numerical response to herbivore density either by being already present in the area when herbivore densities start to increase or by dispersing from nearby or faraway areas early in the growing season (Tscharntke et al. 2007). Fragmentation, fragment age and size, management intensity, and amount of impervious area affect the relative abundance of different trophic groups and result in changes in predator composition and trophic structure (Bolger et al. 2000, Gibb and Hochuli 2002). Finally, both increases in vegetation complexity and nearby natural habitat are positively associated with natural

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enemy abundance in agroecosystems (Uno et al. 2010, Philpott et al. 2014), and may also enhance predator diversity, and potentially predation services and pest control (Letourneau et al. 2009).

Arthropod food-web dynamics of crops commonly found in urban gardens have been widely studied in rural settings, but because urbanization can radically change ecological patterns and processes (Faeth et al. 2005, Shochat et al. 2006) it is unclear whether the vegetation and landscape complexity features that benefit natural enemy communities and efficient pest control services in rural areas will do the same in urban settings. Several factors influence populations and diversity of natural enemies within urban habitats including fragment size, age, shape, microclimatic conditions, productivity, vegetation abundance, richness, and structural complexity (Burkman and Gardiner 2014). Yet, few studies examine what are the implications of habitat differences for predation services, specifically in gardens (e.g., Burkman and Gardiner 2014, Lin et al. 2015). Furthermore, since food-web dynamics are contingent on environmental conditions (Faeth et al. 2005), ecological interactions will likely be altered by imminent management changes in urban gardens such as management turnover, short tenancy periods, and changes in irrigation practices. Urban garden plots are usually under 0.003 ha, whereas the midpoint acreage of U.S. farms in 2007 was 447 ha (MacDonald et al. 2013). Gardening decisions are thus made at small scales. Gardens may also change quickly given that gardeners may be making different management decisions for their individual plots within larger community gardens. Interest in urban gardening has grown tremendously in the past decade, but the impacts of human management decisions on biodiversity and ecosystem services in urban gardens require further study (but see Sattler et al. 2010, Bennett and Gratton 2012, Gardiner et al. 2014, Philpott et al. 2014). While changes in local habitat conditions and landscape surroundings influence particular predator groups (e.g., ants, spiders, parasitoids) in urban settings (Sattler et al. 2010, Bennett and Gratton 2012, Philpott et al. 2014, Otoshi et al. 2015), few studies have examined impacts of local vegetation diversity and complexity and landscape diversity for predation services in urban gardens (Lin et al. 2015, but see Gardiner et al. 2014).

In addition to the scientific knowledge gap about predation services in urban gardens, there is a practical knowledge gap in applying this scientific knowledge to urban agricultural management. In a recent survey that asked 315 urban farmers across 15 U.S. cities about their challenges and training needs, the majority of them expressed significant challenges in managing pests (>90% of surveyed urban farmers) and many also reported critical needs for technical assistance in urban production practices (Oberholtzer et al. 2014). In addition, some gardener surveys report that pest populations can often exceed economic damage thresholds, and because gardeners do little to control pests, that insect pests continue

to be a large challenge (Gregory et al. 2016). Thus, even though these critical needs abound in urban agroecosystems, we lack the scientific expertise to inform urban farmers and gardeners about how their production and management practices impact pest control and other ecosystem services. This missing knowledge is especially concerning given increasing global food demands, increased climate-induced ecosystem stress, and the increasing importance of urban agriculture for providing for food security, especially in communities where food access is quite limited (Pothukuchi and Thomas 2004, Rocha 2007, Ver Ploeg et al. 2009, Chappell and LaValle 2011). Currently >80% of the U.S. population lives in urban areas (U.S. Census Bureau 2014) and by 2030, 80–90% of the global population will live in cities (United Nations 2005, Seto et al. 2012). Urban residents increasingly are using urban gardens in order to produce food (Alig et al. 2004).

In this study, we examined the local and landscape drivers of predation services in urban gardens. The distinction between local-scale and landscape-scale factors may be defined by the taxon of interest in a study, as different organisms respond to habitat changes at different spatial scales depending on their dispersal abilities or resource requirements (e.g., Fahrig et al. 2011, Gonthier et al. 2014). In this study, we characterize local- vs. landscape-scale characteristics based on garden management, rather than examining the dispersal characteristics of garden pests or predators. Specifically, we take local scale factors to be those which gardeners can manipulate within their plots, or collectively at the community garden level (e.g., crop and non-crop plant diversity, tree and shrub abundance and richness, ground cover characteristics), and landscape-scale characteristics to be features that change outside of the garden boundaries (e.g., different land cover types within 1 km, landscape diversity). We specifically aimed to answer the following two questions: (1) Do predators remove a significant portion of prey items introduced into gardens? (2) Do local management characteristics of gardens or landscape surroundings influence the effectiveness of predation services? We aimed to elucidate ecological patterns of predation services in urban gardens, and to determine key local management and landscape changes that may result in increases in biological control of pest species in urban gardens.

METHODS

Study design and local and landscape characteristics

We worked in 19 urban garden sites between 444 and 15525 m² that were separated by at least 2 km in three counties (Santa Cruz, Santa Clara, and Monterey) in the central coast of California (Fig. 1). All gardens had been actively cultivated between 5 and 47 yr. We measured local habitat characteristics within a 20 × 20 m plot in each garden. We measured canopy cover with a convex

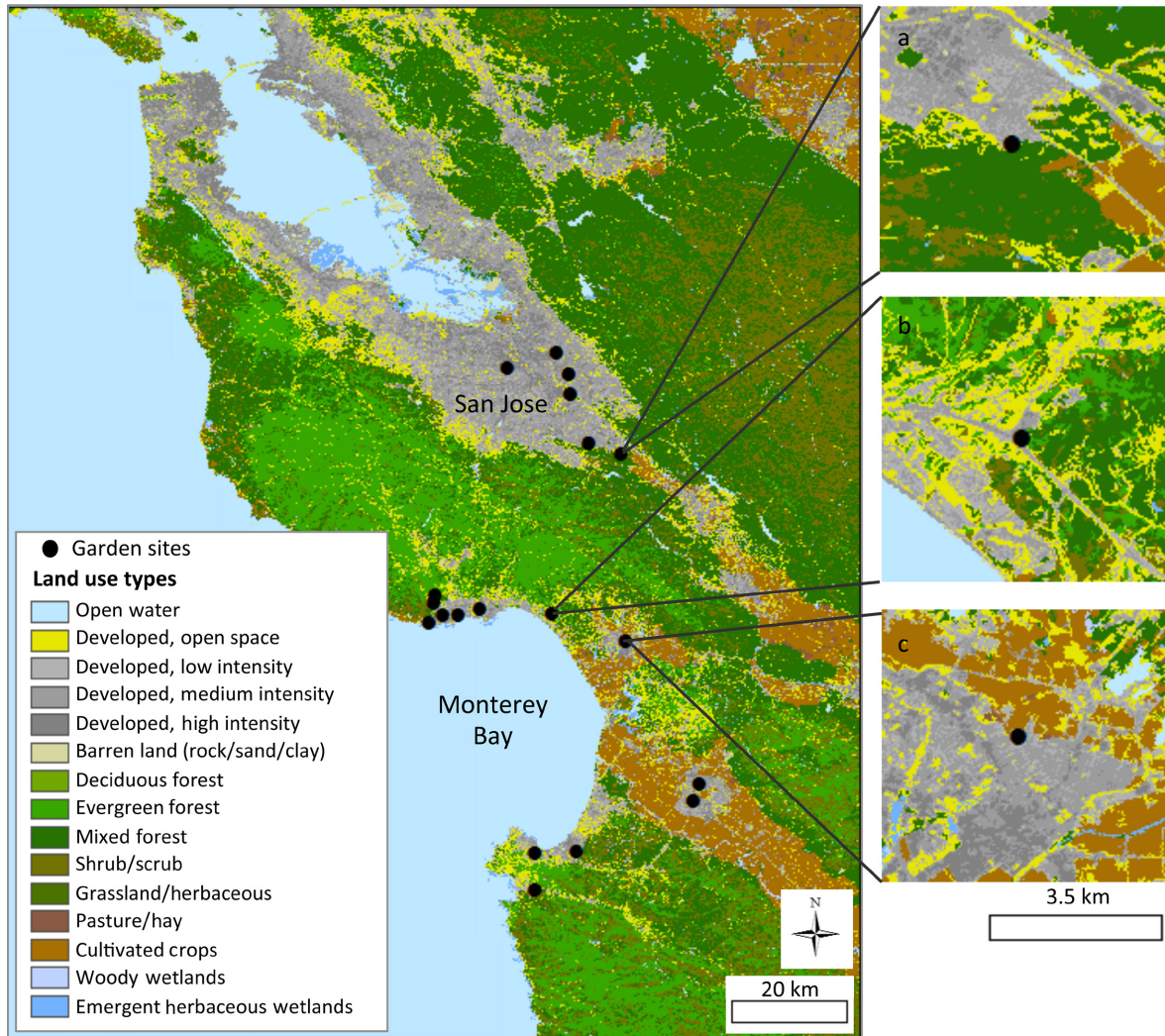


FIG. 1. A map of the Central coast region of California showing the 19 urban garden sites in Monterey, Santa Clara, and Santa Cruz Counties, and land cover types in the study region and surrounding the garden study sites. Three inset panels show (a) a garden surrounded primarily by urban and natural land, (b) a garden surrounded by natural, open, and urban land, and (c) a garden surrounded by primarily urban and agricultural land.

spherical densitometer at the plot center, and 10 m to the N, S, E, and W. We counted and identified all trees and shrubs, and noted the number in flower. In four 1×1 m plots within 20×20 m plots, we measured the height of the tallest non-woody vegetation, counted flowers, and measured ground cover from bare soil, grass, herbaceous plants, rocks, leaf litter, and mulch or straw. All herbaceous plants (except grasses) were identified to morphospecies, and classified as crops, weeds, or ornamentals. Within 100×100 m plots around gardens, we counted all trees (>30 cm circumference at breast height) and quantified percent area with concrete and buildings, bare ground, mulch, lawn, woody vegetation, and weedy or non-woody vegetation. We measured 20×20 m and 1×1 m plot variables twice during 2 yr (28–30 July and 19–21 August 2014 and 2 August and 1–3 September

2015), within a few days of prey removal experiments. We measured all 100×100 m variables once, in September 2014. We averaged values for variables measured multiple times. Thus we measured 24 local habitat features for each garden (Table S1).

We classified the landscapes surrounding each garden with land cover data from the 2011 National Land Cover Database (NLCD, 30 m resolution; Homer et al. 2015) and calculated percent of land cover types in 1-km, 2-km, and 5-km buffers around each garden with spatial statistics tools in ArcGIS v. 10.1 (Esri, Redlands, California, USA). We chose three spatial scales as different predator taxa respond to landscape change at different scales (Egerer et al. 2017). We used NLCD land cover types to create four landscape categories: (1) natural (including deciduous [NLCD number 41], evergreen [42], and mixed

forests [43], dwarf scrub [51], shrub/scrub [52], and grassland/herbaceous [71]), (2) open (including lawn grass, park, and golf courses [21]), (3) urban (including low- [22], medium- [23], and high-intensity developed land [24]), and (4) agriculture (including pasture/hay [81] and cultivated crop [82]). Other land cover types covered <5% of the surrounding landscape and were not included. We used the *vegan* package in R (Oksanen 2015) to calculate landscape diversity (e.g., modified Shannon-Wiener diversity index, H') for each garden at 1, 2, and 5 km scales (McGarigal et al. 2002, Bennett and Gratton 2012). As land cover type richness and evenness (weighted representation of land cover types) increases, the H' values increase, showing higher landscape diversity. We calculated a total of 15 landscape variables for the analysis (see Appendix S1: Table S1).

Predation services experiments

To estimate predation services provided by naturally occurring predator species in gardens, we conducted sentinel pest experiments with three types of prey: (1) corn worm eggs (*Helicoverpa zea*), (2) pea aphids (*Acyrtosiphon pisum*), and (3) cabbage looper larvae (*Trichoplusia ni*). We purchased eggs and larvae from Frontier Agricultural Sciences in Newark, Delaware, USA and aphids from Berkshire Biological in Westhampton, Massachusetts, USA. Eggs were stored in the freezer prior to experiments. Larvae were purchased immediately prior to experiments, reared on artificial diet until they reached the fourth instar, and then used in experiments. Aphids were reared on covered fava bean (*Vicia faba*) plants in the Thimann Greenhouse at UC Santa Cruz until populations reached ~600–1200 aphids per plant. All insects were purchased and transported under USDA-Aphid permit P526P-14-02660, and all insects were destroyed after experiments were concluded.

For field experiments, prey were placed on potted, greenhouse-raised fava bean plants (25–30 cm tall) in either open (predator access) or bagged (predator exclusions) treatments. Eggs were laid on cloth sheets and we cut cloth into 1 × 1 cm squares, counted all eggs, pinned one square each to two different branches of one fava plant, and bagged one branch. We placed two fava bean plants with aphids in each garden, counted aphids, and bagged one plant. We placed 8–10 larvae on each of two fava bean plants per garden, and bagged one plant. We placed plants in random locations in each garden, with open and bagged treatments placed in the same spot. We returned 24 h later to retrieve plants and to recount eggs, aphids, and larvae. We noted whether any predators were present inside bags (i.e., exclusion treatments were ineffective) and did not include those replicates in the analysis. We conducted predation services experiments between 21–24 July and 25–27 August 2014 (aphids and eggs) and between 31 July–1 August and 9–10 September in 2015 (all prey species).

Data analysis

We divided explanatory variables into biologically relevant groups: (1) woody vegetation factors, (2) herbaceous plant richness, (3) ground cover in 1 × 1 m plots, (4) ground cover in 100 × 100 m plots, and (5) landscape factors and ran Pearson's correlations to identify correlated variables within groups, and reduce the overall number of variables and select variables for subsequent analysis (see Appendix S1: Table S2). We selected the variables in each group with either the largest number of significant correlations ($P < 0.05$) or the highest correlation coefficients, as well as variables that were not correlated with others. Two other variables (number of flowers, garden size) were not included in any group and were selected. In all, 10 local variables and 3 landscape variables were selected (see Appendix S1: Table S2). We used natural log (garden size, number trees and shrubs, number of flowers, number of herbaceous plant species) or square root transformed data for analysis (rock, leaf litter, and mulch cover in 1 × 1 m plots, and concrete and buildings and bare soil cover in 100 × 100 m plots).

We used two response variables for predation services: (1) proportion of prey removed from open treatments, and (2) predation effect size (log response ratio, LRR). Predation effect size was calculated as $\ln(\text{proportion prey removed in open treatments}) - \ln(\text{proportion of prey removed in bagged treatments})$ for each site, where higher values indicate higher removal of prey items from open relative to bagged plants. We examined differences in response variables for each prey species in different sample periods (all prey species) and years (aphids, eggs) with generalized linear mixed models (GLMM) with period (early, late) and year (2014, 2015) as fixed factors, and site as a random factor. There were no differences in period or year for proportion of prey items removed (see Appendix S1: Table S3). Egg predation effect size differed with period, larvae predation effect size differed with period, and aphid predation effect size did not differ with period or year (see Appendix S1: Table S3). As we aimed to examine general prey removal patterns, we averaged proportions and effect sizes across period and year for other analyses.

To examine whether predators effectively remove prey from urban gardens, we compared the proportion of prey (eggs, aphids, or larvae) removed in open vs. bagged plants with GLMM with treatment (open vs. bagged) as the fixed factor and site as a random factor. To examine which local and landscape factors drive prey removal in urban gardens, we used generalized linear models (GLMs) with the *glm* function in R (R Development Core Team 2014). We included the predation effect sizes for aphids, eggs, and larvae as response variables, and tested all combinations of the 13 selected explanatory variables with the *glmulti* package (Calcagno and de Mazancourt 2012). We selected the top model based on the AIC_c values. For models where the AIC_c for top

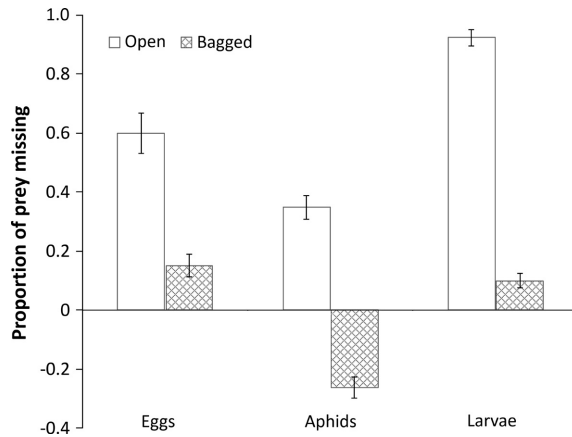


FIG. 2. Results of predation experiments conducted in 19 urban gardens in the California central coast in 2014 and 2015. Bars show proportions of prey (corn worm eggs, pea aphids, and cabbage looper larvae) missing (mean \pm SE) from open and bagged (predator exclusion) fava bean plants after 24 h. Differences between treatments are significant for all prey items (t test, $P < 0.05$).

models was within 2 points of the next best model, we averaged models (up to the top 10 models) with the MuMIn package (Barton 2012) and report conditional averages for significant model factors. We used the Gaussian family as all response variables were normally distributed, and we checked model fits with QQ plots and Shapiro-Wilk tests. We graphed all significant local and landscape predictors of prey removal with the visreg package in R (Breheny and Burchett 2013).

RESULTS

Overall, predation services across all gardens were high, and there were strong differences between open and bagged treatments, indicating significant predation (Fig. 2). In

bagged treatments, aphid populations grew, but ~40% of aphids were missing from open plants after 24 h ($F_{1,18} = 122.6$, $P < 0.0001$). The proportion of eggs missing was three times higher in open treatments compared with bagged treatments ($F_{1,18} = 40.25$, $P < 0.0001$). Nearly all larvae were missing from open plants, whereas fewer than 20% were missing from bagged plants ($F_{1,17} = 662.2$, $P < 0.0001$).

Predation effect sizes were driven by many local and two landscape factors, but the specific drivers varied with prey species. The model that best predicted egg predation included garden size and number of trees and shrubs (Akaike's information criterion, $AIC = -14.78$, ΔAIC for next best model = 4.73, $df = 16$, $R^2 = 0.59$; see Appendix S1: Table S4). Egg predation was higher in small gardens ($P = 0.019$, Fig. 3a) and in gardens with high tree and shrub abundance ($P = 0.003$, Fig. 3b). The model that best predicted aphid predation included garden size, number of trees and shrubs, number of herbaceous plant species, mulch and leaf litter cover (in 1×1 m plots), concrete cover (in 100×100 m plots), and landscape diversity ($AIC = -57.49$, ΔAIC for next best model = 4.15, $df = 11$, $R^2 = 0.86$; see Appendix S1: Table S4). Aphid predation increased in gardens with more litter cover ($P = 0.005$, Fig. 4a) and more trees and shrubs ($P < 0.0001$, Fig. 4b) and was lower in large gardens ($P < 0.0001$, Fig. 4c), in gardens with more mulch ($P < 0.0001$, Fig. 4d), with higher herbaceous plant richness ($P = 0.003$, Fig. 4e), with more concrete and buildings ($P < 0.0001$, Fig. 4f), and with higher landscape diversity ($P = 0.0002$, Fig. 4g). The model that best predicted larvae predation included number of trees and shrubs, rock and leaf litter cover (in 1×1 m plots), and the amount of agriculture within 2 km of gardens ($AIC = -44.25$, ΔAIC for next best model = 8.515, $df = 13$, $R^2 = 0.72$; see Appendix S1: Table S4). Larvae predation increased in gardens with more leaf litter ($P = 0.039$, Fig. 5a) and more rocks ($P = 0.002$,

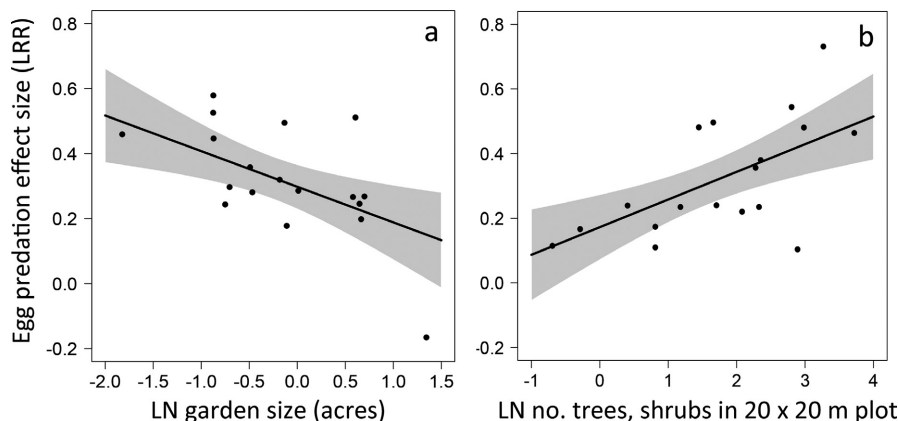


FIG. 3. Drivers of egg predation effect sizes in urban gardens in the California central coast. Egg predation effect size was calculated as the log response ratio ($LRR = [\ln(\text{proportion of eggs removed in open treatments})] - [\ln(\text{proportion of eggs removed in bagged treatments})]$). According to generalized linear models, egg predation varied with (a) garden size and (b) number of trees and shrubs within 20×20 m plots. Higher effect sizes indicate higher removal in open compared with bagged plants. All graphed factors are significant at the $P < 0.05$ level. Shaded areas are 95% confidence bands.

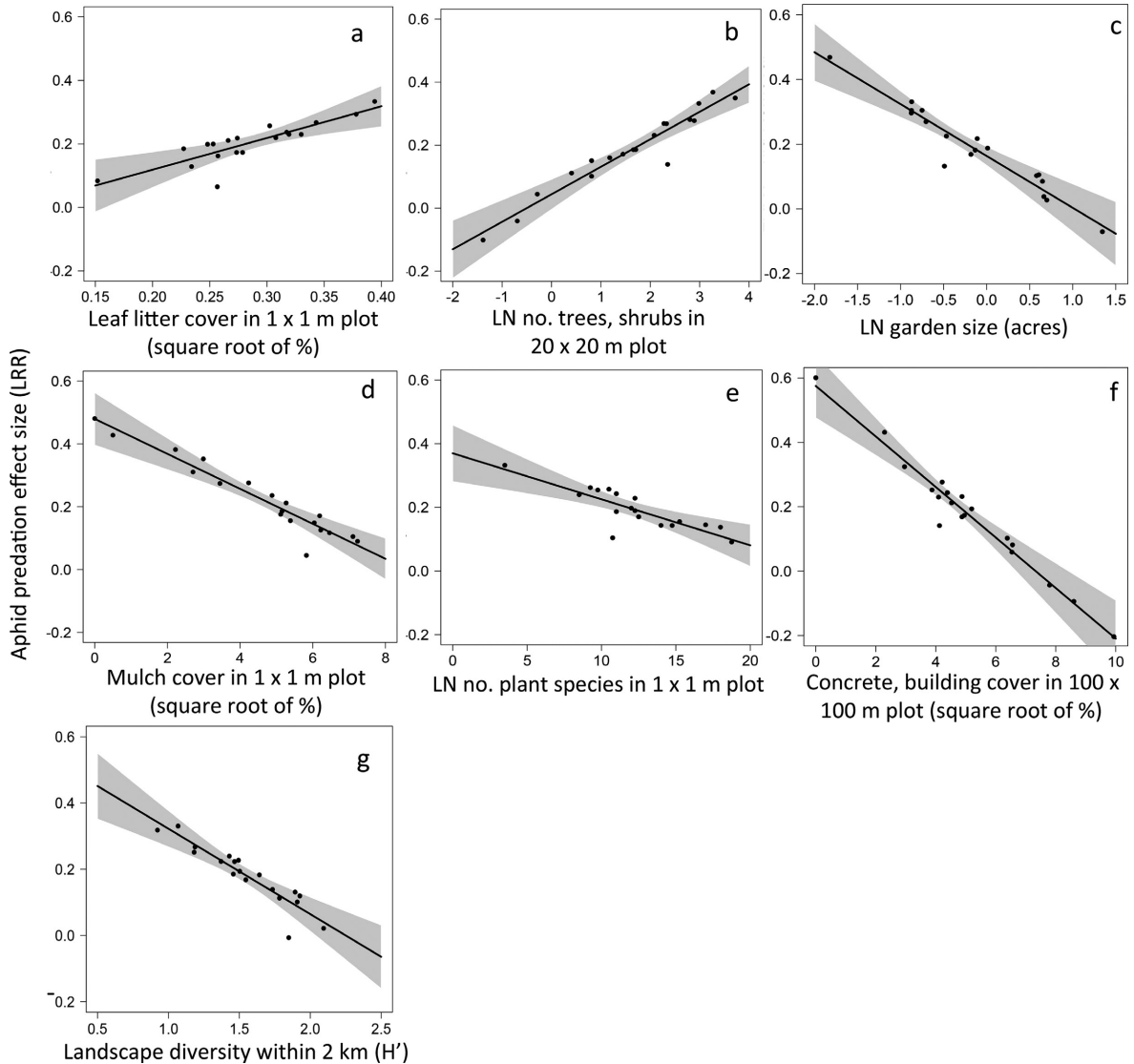


FIG. 4. Drivers of aphid predation effect sizes in urban gardens in the California central coast. Aphid predation effect size was calculated as the log response ratio ($LRR = \ln[\text{proportion aphids removed in open treatments}] - \ln[\text{proportion of aphids removed in bagged treatments}]$). According to generalized linear models, aphid predation varied with (a) leaf litter in 1×1 m plots, (b) number of trees and shrubs within 20×20 m plots, (c) garden size, (d) mulch in 1×1 m plots, (e) number of herbaceous plant species, (f) concrete and building cover in 100×100 m plots, and (g) landscape diversity (H') within a 2-km radius. Higher effect sizes indicate higher removal in open compared with bagged plants. All graphed factors are significant at the $P < 0.05$ level. Shaded areas are 95% confidence bands.

Fig. 5b) but decreased in gardens with more trees and shrubs ($P = 0.016$, Fig. 5c) and in gardens surrounded by more agriculture ($P < 0.0001$, Fig. 5d).

DISCUSSION

First, we investigated whether a significant proportion of prey were removed from gardens and found strong evidence that prey quickly disappeared. At least half of the eggs and almost all of the larvae were missing after just 24 h, and aphid population growth was significantly

slowed in open treatments compared with bagged treatments. We did not collect data on predator identity but, when putting out and picking up treatment plants, we saw Argentine ants (*Linepithema humile*) and spiders on eggs, observed adults and larvae of lady beetles (e.g., *Harmonia axyridis*, *Coccinella septempunctata*, and *Hippodamia convergens*) on plants with aphids, and saw vespid wasps, birds, and wolf spiders remove larvae. Thus several predator taxa likely remove potential pests from urban gardens. The few others that have examined prey removal in gardens also experience fast and high

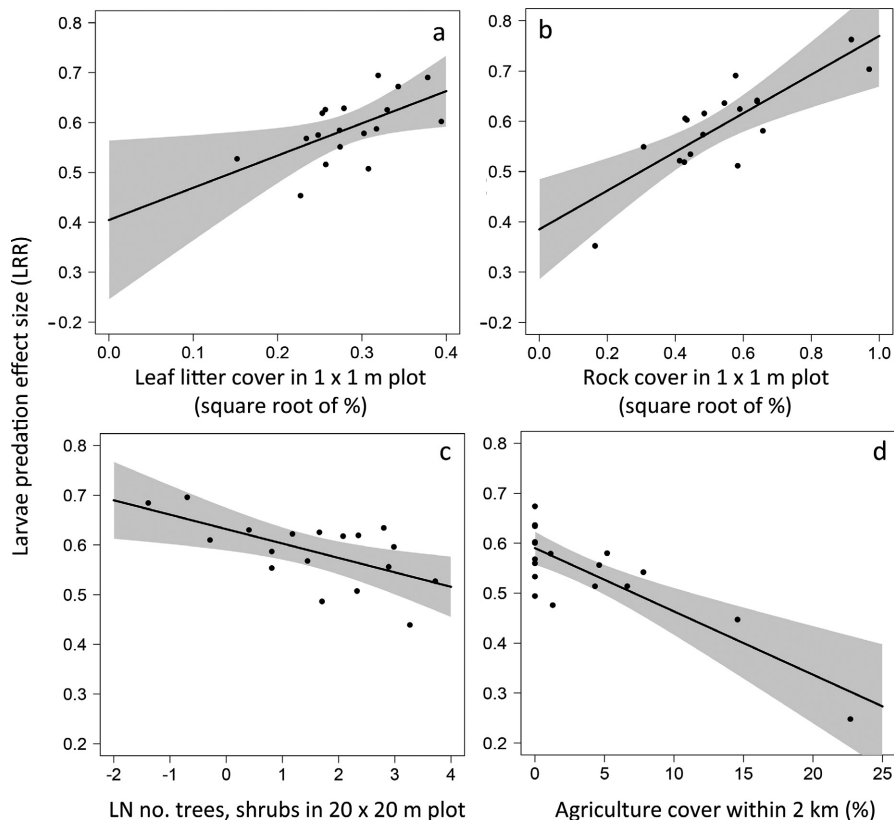


FIG. 5. Drivers of larvae predation effect sizes in urban gardens in the California central coast. Larvae predation effect size was calculated as the log response ratio ($LRR = \ln[\text{proportion larvae removed in open treatments}] - \ln[\text{proportion of larvae removed in bagged treatments}]$). According to generalized linear models, larvae predation varied with (a) leaf litter cover in 1×1 m plots, (b) rock cover in 1×1 m plots, (c) number of trees and shrubs within 20×20 m plots, and (d) amount of agriculture within a 2 km radius. All graphed factors are significant at the $P < 0.05$ level. Shaded areas are 95% confidence bands.

removal rates. Removal of moth eggs and fly pupae is high in both urban gardens and vacant lots (Gardiner et al. 2014). Likely, such high predation services are maintained in urban gardens due to presence of generalist and disturbance-tolerant species, rather than specialist natural enemies (Burkman and Gardiner 2014). Identifying the relationships between specific prey items and their predators, as well as the impacts of specific management practices on predator-prey interactions may be an interesting direction for future study.

Second, we examined which local and landscape factors drive predation services in urban gardens. Among local factors, we found that vegetation structure and diversity (measured by woody plant abundance and richness as well as richness of herbaceous vegetation), garden size, and ground cover features affected predation services. Significant landscape-level factors were landscape diversity and agriculture within 2 km. However, effects differed with prey species.

Vegetation structure and diversity had both positive and negative effects on predation. In urban systems, higher vegetation and structural complexity may provide alternative prey items and more stable resources for

generalist predators, higher predator abundance, and increased prey removal (Shrewsbury and Raupp 2000, Raupp et al. 2009). In our study, tree and shrub abundance enhanced egg and aphid predation, but negatively affected larvae predation. In our study sites, abundance of ants, spiders, and lady beetles (potential predators of eggs and aphids) increases with tree and shrub abundance and canopy cover (Otoshi et al. 2015, Egerer et al. 2016; S. M. Philpott, *unpublished data*), and in other habitats spider abundance increases with structural complexity (Shrewsbury and Raupp 2000, Langellotto and Denno 2004). Thus higher tree abundance may have increased predator abundance and thus egg and aphid predation. We are not aware of any studies examining changes in wasp (larvae predators) abundance or richness in gardens. Abundance of insectivorous birds (larvae predators) may increase in gardens with higher vegetation diversity (Lim and Sodhi 2004, Paker et al. 2014). Yet, increases in vegetation structure may provide more arboreal insect resources for birds (Lim and Sodhi 2004) that may result in increased bird foraging time in trees, rather than in garden-level herbaceous vegetation. Other nuanced changes in garden vegetation may also affect the

bird community. For example, insectivore composition and richness differs in sites with native vs. exotic arboreal vegetation (White et al. 2005) and both richness and abundance of insectivores is nearly double in suburban areas with native (vs. nonnative) plant landscaping (Burghardt et al. 2008). We did not examine woody plant communities to this detail, but related changes may explain differences in the insectivores, and thus larvae predation services.

We found that herbaceous plant richness was negatively associated with aphid removal. Increases in plant diversity in urban gardens can benefit beneficial insect diversity (Bennett and Gratton 2013), leading to increases in predation. But not all studies find positive relationships between vegetation complexity and predation. For example, Bennett and Gratton (2012) found that floral diversity was negatively correlated with removal of sentinel pests. In our study gardens, lady beetle richness increases with crop diversity, a factor positively correlated with herbaceous plant richness in our sites (Egerer et al. 2016). Predator richness may lead to interference competition between species, and negatively impact pest control, as is often observed between *Harmonia axyridis*, a common exotic species, and other lady beetle species (Alyokhin and Sewell 2004, Snyder et al. 2004, Brown et al. 2011). Thus increased lady beetle richness in more diverse gardens may be responsible for the negative association between plant diversity and aphid predation.

Garden size significantly impacted egg and aphid predation, with higher removal in smaller gardens. One reason may be that smaller fragments support higher populations of some predators. In southern California, small coastal scrub fragments support higher populations of spiders, carabid beetles, and Argentine ants, and predator species composition also differs with fragment size (Bolger et al. 2000); parallel changes in populations of these predators may have influenced egg removal rates at our study sites. In addition, ant richness declines in smaller fragments (Yamaguchi 2004, Holway and Suarez 2006), often due to increases in the abundance of aggressive exotic ants that may nonetheless be effective predators. Lady beetle abundance, richness, and ability to control aphid pest outbreaks may be affected by fragment size (With et al. 2002) and surrounding landscape (Bianchi et al. 2006). In our study sites, lady beetle species richness is higher in smaller gardens, but only in sites with little natural habitat in the surrounding areas (Egerer et al. 2016), and higher richness may negatively affect predation services provided by lady beetles. Additionally, changes in fragment size might differentially influence species that differ in predation services provided.

Different ground cover features had positive and negative effects on predation. Aphid and larvae predation increased with leaf litter cover, larvae predation increased with rock cover, and aphid removal declined with mulch cover and concrete and building cover. On average, leaf litter cover is low, as most trees and shrubs are at the

garden edges. In all 1×1 m plots except one, leaf litter cover was less than 25% cover and on average only ~14% cover across all plots. Leaf litter may create microhabitats or microclimates that benefit certain predators. Most mulch in the garden sites is wood chip mulch that may provide very different resources from leaf litter from trees and shrubs. We have observed higher lady beetle richness in sites with less mulch (Egerer et al. 2016), and higher lady beetle richness may lead to higher predation if species have complementary foraging patterns or strategies, although this is contrary to the effects of interspecific competition proposed above. In contrast, spiders benefit from mulch cover (Otoshi et al. 2015), perhaps due to lower predation risk to spiders, or perhaps lower movement rates that might allow spiders to more effectively hunt prey. Overall, it is unclear how the changes in leaf litter or mulch cover may influence predation but may be due to changes in refuges, prey availability, or abundance or richness of natural enemies. Generally urbanization negatively affects arthropods (e.g., McIntyre 2000) and might explain lower predation rates in areas with high concrete cover. Low predation rates on aphids in areas with high concrete and building cover could be due to direct effects of temperature on aphid population growth, rather than low removal; some urban herbivores may respond more strongly to temperature increases associated with impervious surface than to top down effects of natural enemies (Dale and Frank 2014). However, predators, including lady beetles, may be more abundant near to buildings (Nalepa et al. 2004, Philpott et al. 2014).

Finally, landscape diversity and agriculture in the surrounding landscape negatively correlated with predation. Aphid predation declined with increases in landscape diversity. Declines in predation with landscape complexity is a highly contradictory result to that of Gardiner et al. (2009) who found that predation on soybean aphids by generalist predators (including coccinellids) increased significantly with landscape diversity, and higher natural habitat in the landscape in rural areas of the north-central United States. Indeed, several studies have documented higher predation and parasitism in more complex landscapes (Bianchi et al. 2006, 2008, Thies et al. 2008, Boccaccio and Petacchi 2009). There is overwhelming evidence that natural enemies benefit from landscape complexity and that herbivores do not, and some argue that these measures should be more effective determinants of pest control (Chaplin-Kramer et al. 2011). Thus, our data provide a very important example of how ecological and trophic interactions may respond very differently to landscape change in urban vs. rural landscapes. In other words, landscape complexity may mean something very different for predator-prey interactions within the urban context. Surprisingly, urban cover (negatively correlated with natural and open habitat) did not influence predation services at all, despite many studies that implicate urbanization in arthropod changes. Compared with some other urban or even rural habitats, gardens may offer

more productive environments and more resources for predators than surrounding areas, especially during periods of drought (Faeth et al. 2005) such as that experienced in the California Central Coast in the 4 yr during and prior to the study. We also found that amount of agriculture in the surrounding landscape negatively correlated with larvae removal. Spider and wolf spider abundance in gardens increases with agricultural area in the landscape, albeit at smaller spatial scales (500 m; Otoshi et al. 2015), so a reduction in predation is likely not due to declines in spider abundance. In contrast, bird abundance may decline with an increase in agriculture. Birds in urban or peri-urban environments benefit from presence of trees (Lim and Sodhi 2004, Paker et al. 2014). Agricultural areas in the study region are increasingly devoid of arboreal vegetation (e.g., Karp et al. 2015) and may not support high bird populations or thus larvae removal in landscapes with high agriculture cover.

Urban gardens frequently suffer from pest populations that exceed economic damage thresholds, and gardeners do little to control pests (Gregory et al. 2015), perhaps due to a lack of technical assistance, a lack of knowledge about pest management (Oberholtzer et al. 2014), or perhaps a lack of knowledge or concern about the economic damage thresholds. We provide new information about predation services within urban gardens. We report that there are resident predators likely from a number of taxa that occur within urban gardens and naturally control common garden pests. In addition, several local habitat features that gardeners can manipulate in the short (mulch cover, litter cover, etc.) and long term (number of trees and shrubs) may increase the effectiveness of predation services within their gardens. Indeed, we found that 70% of the local factors appeared in the best models predicting predation. Thus predation services in urban gardens likely depend on local garden management, related shifts in abundance and richness of herbivores and natural enemies, composition of natural enemies, and trophic interactions between predators and herbivores. Understanding the effects of local factors may be more important from a management standpoint, as gardeners can manipulate their garden plots, or can work in groups to manipulate ornamental or arboreal plant abundance and richness within gardens. Landscape changes likely require more involvement of municipal authorities and the larger community. However, 66% of the three landscape factors also appeared important for prey removal, highlighting their simultaneous importance. Our intent was to examine how habitat manipulation, rather than changes in the abundance and richness of herbivore or natural enemies, directly affects predation services. From an ecological standpoint, understanding mechanisms responsible for changes in predation services is critical for conservation of natural enemies as well as provisioning of ecosystem services. But from a practical standpoint, understanding how local habitat manipulation affects predation and biological control of garden pests, in which landscape conditions, is critical for gardeners.

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SUPPORTING INFORMATION

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DATA AVAILABILITY

Data associated with this paper have been deposited in a Dryad digital repository <https://doi.org/10.5061/dryad.mn8b2>