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Authors

Egerer, Monika H
Liere, Heidi
Lin, Brenda B
et al.

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Herbivore regulation in urban agroecosystems: Direct and indirect effects

Monika H. Egerer[a],*, Heidi Liere[b], Brenda B. Lin[c], Shalene Jha[d], Peter Bichier[a],
Stacy M. Philpott[a]

[a]*Environmental Studies Department, University of California, Santa Cruz, Santa Cruz, CA 95064, USA*
[b]*Biology Department, Reed College, Portland, OR 97202, USA*
[c]*CSIRO Land and Water Flagship, Aspendale, VIC 3195, Australia*
[d]*Integrative Biology Department, University of Texas at Austin, Austin, TX 78712, USA*

Abstract

Urban agroecosystems can provide habitat for biodiversity and can benefit human communities through urban food provisioning. Moreover, urban agroecosystems could be managed so as to optimize ecosystem services like natural pest control provided by trophic interactions between natural enemies and herbivores. As in other ecosystems, predation and parasitism regulate herbivores in urban settings, but less is known about the relative importance of direct and indirect effects at local and landscape scales in highly managed urban agroecosystems. We collected data on herbivore (cabbage aphid) density and parasitism ratios (proportion of parasitized aphid "mummies") in 25 community gardens in three counties in the California central coast, USA. We used structural equation modeling to examine the effects of direct factors (host plant characteristics and parasitism) and indirect factors (soil, garden, and landscape characteristics) on herbivore density changes at two time points in the growing season (June and August). Aphid density, but not parasitism, varied across counties over the season, and there was a strong negative relationship between aphid density and parasitism. Direct effects were strong drivers of aphid density but not parasitism. In June, aphid density increased with host plant volume but decreased with greater floral density, while parasitism was only influenced by aphid density. In August, host plant volume similarly positively affected aphid density, and soil water holding capacity increased host plant volume. In addition, host plant density had a strong negative effect on parasitism. Urban gardeners may be able to reduce aphid pest densities by increasing floral resource density and strategically spatially distributing host plants throughout garden beds, though these processes depend on the season. The indirect effects of soil water holding capacity on aphid densities further suggest a critical role of human management on pest populations and pest control services through soil amendments and irrigation.

Introduction

Drivers of trophic interactions among predators and their prey may be fundamentally different in urban ecosystems from natural systems due to the anthropogenic alteration

*Corresponding author.
E-mail addresses:* megerer@ucsc.edu (M.H. Egerer), heliere@reed.edu (H. Liere), Brenda.Lin@csiro.au (B.B. Lin), sjha@austin.utexas.edu (S. Jha), pbichier@ucsc.edu (P. Bichier), sphilpot@ucsc.edu (S.M. Philpott).

of local resource availability and urban landscape structure (Shochat et al., 2010). Plant nutrient and water availability, for example, are usually heavily supplemented in cities, thus reducing resource limitation for herbivores (Raupp, Shrewsbury, & Herms, 2010). Local vegetation simplification and habitat disturbance, fragmentation, and isolation that are characteristic of urban ecosystems (Faeth, Warren, Shochat, & Marussich, 2005; Niemelä, 2011) can strongly influence organisms in higher trophic levels (Marzluff, 2001; Burkman & Gardiner, 2014) to potentially alter interactions between herbivores and plants (Nelson & Forbes, 2014).

In particular, urban agroecosystems like community (i.e., allotment) gardens offer a model system in which to examine how changes in local management factors and surrounding landscape features affect insect communities and their interactions. In contrast to other urban ecosystems like turf-grass dominated parks managed by the city or private home gardens managed by individuals, urban community gardens are unique in that they have multiple plot holders and generally have high local vegetation complexity and high diversity of management practices (Guitart, Pickering, & Byrne, 2012). Furthermore, urban agroecosystems are usually small habitats isolated from one another and from other natural habitats (Faeth et al., 2005). Moreover, ecological knowledge gained from garden studies has practical application because bans on synthetic pest control inputs (e.g., organophosphates, pyrethroids) in many community gardens require efficient natural pest control of herbivores by natural enemies for urban agricultural sustainability (Oberholtzer, Dimitri, & Pressman, 2014).

Environmental factors such as local vegetation composition and complexity, as well as the amount of impervious cover (i.e., concrete and built surfaces) in the urban landscape can directly and indirectly affect higher trophic interactions like parasitism of herbivores across spatial scales (Pereira-Peixoto, Pufal, Staab, Martins, & Klein, 2016; Fenoglio, Werenkraut, Morales, & Salvo, 2017). For example, as predicted by the *resource concentration hypothesis* (Root, 1973), high host plant density in urban yards and parks increases the likelihood of pest outbreaks by directly increasing resource availability for herbivores (Dreistadt, Dahlsten, & Frankie, 1990; Shrewsbury & Raupp, 2006; Shrewsbury & Raupp, 2000). Similarly, as predicted by the *plant stress hypothesis* (White, 1969), soil nutrient and irrigation management can indirectly affect sap-sucking herbivore populations by altering host plant quality (Mattson, 1980; Hanks & Denno, 1993). These local-level factors can also have indirect effects on herbivore populations by altering the abundance, species composition, and the foraging behavior of their natural enemies (Hanks & Denno, 1993; Shrewsbury & Raupp, 2000, 2006). For example, *sensu* the *enemies hypothesis*, natural enemies should be more abundant and herbivore regulation more effective by delivering greater pest mortality in more structurally complex habitats with, for example, diverse vegetation (Root, 1973). Indeed, parasitism in urban contexts has been shown to increase with increasing habitat complex-

ity through greater natural enemy richness in those habitats (Fenoglio, Videla, Salvo, & Valladeres, 2013).

Likewise, landscape-level factors, such as the amount of impervious cover, may directly affect herbivores through changes to micro-climate (e.g., heat island effects) and atmospheric conditions (Newman, 2003) and habitat isolation (Turrini, Sanders, & Knop, 2016). The amount of impervious cover can also indirectly affect herbivores by altering the populations and communities of their natural enemies (Bennett & Gratton, 2012a; Burkman & Gardiner, 2014) who may differ in sensitivity to urbanization (Fenoglio, Salvo, & Estallo, 2009; Fenoglio et al., 2013). For example, landscape-level environmental factors may subsequently change natural enemy-herbivore interactions (Shrewsbury & Raupp, 2000) and natural pest control provided by natural enemies through direct predation (Philpott & Bichier, 2017) and parasitism (Pereira-Peixoto et al., 2016). In sum, herbivore populations in urban community gardens can be affected by local factors through direct effects (e.g., by changing the availability and quality of their food) or through indirect ones (e.g., by changing the abundance of their natural enemy), as well as by landscape factors through direct effects (e.g., impervious cover can hinder their colonization to and from suitable habitats) or indirect ones (e.g., impervious cover can act as a colonization barrier to their natural enemies).

The strength of these direct and indirect effects may experience seasonal changes. The abundance and diversity of arthropod natural enemies can decrease over time in response to fluctuations in precipitation and temperatures (Bolger et al., 2000), and this can affect herbivore regulation through resource availability (Faeth et al., 2005). Moreover, the seasonal fluctuations that affect population-level resource availability and environmental stressors are combined with direct effects from human activities in cities that alter resources (Faeth et al., 2005). The altered patterns in resources and stressors due to temporal change and anthropogenic change can impact ecological predictions organized around direct versus indirect effects, resource concentration versus natural enemy regulation, at local versus landscape scales in urban systems (Dale & Frank, 2014). Thus even though we are beginning to understand the local and landscape factors that regulate herbivores through parasitism in urban systems (Fenoglio et al., 2013; Pereira-Peixoto et al., 2016), we still lack an understanding of local, landscape, and temporal factors in urban agroecosystems compared to rural agricultural landscapes.

In this study we aimed to investigate how local and landscape factors directly and indirectly affect insect herbivore regulation in urban agroecosystems (community gardens). We focus on the regulation of aphid herbivores – a prevalent sap-sucking pest in gardens – through parasitism by parasitic wasps as a trophic interaction that provides pest control services. Specifically, we asked: (1) How do local garden management factors (host plant characteristics, floral resources, and soil properties) and the landscape context of gardens (amount of surrounding impervious cover) affect
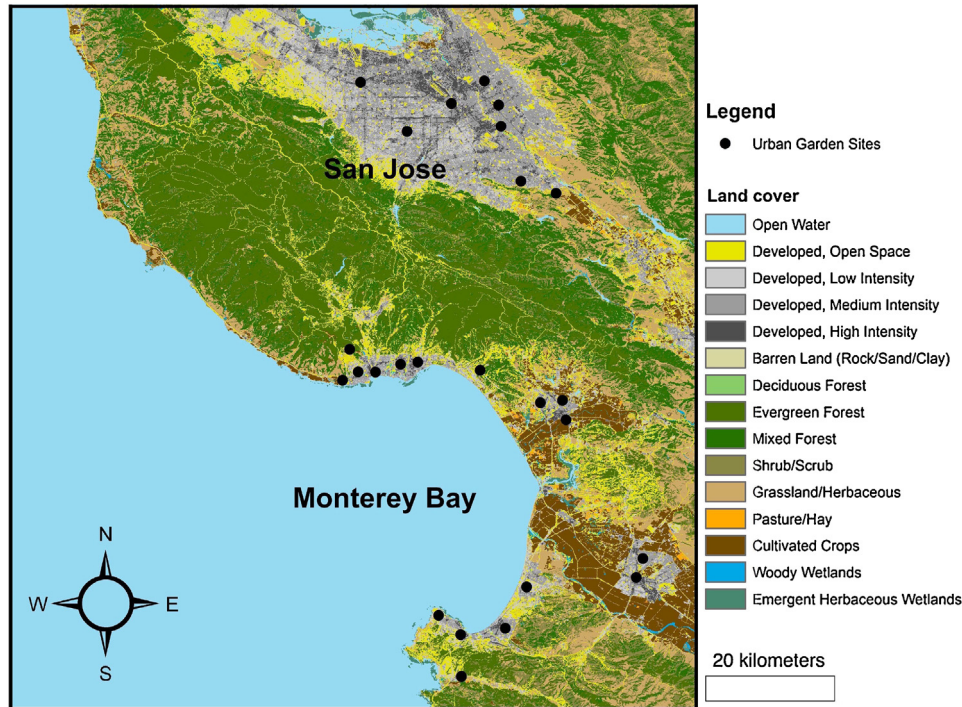
Fig. 1. Map of the California central coast, USA showing the 25 urban community garden sites in Monterey, Santa Cruz, and Santa Clara counties. The gardens are surrounded by different land cover types as classified by the US Geological Survey's National Land Cover Database.

herbivore abundance through direct effects on herbivore density and indirect effects by affecting herbivore parasitism? (2) Does the importance of these effects change with time?

Materials and methods

Study system

We worked in 25 community gardens in three counties in the California central coast, USA: Monterey (36.2400° N, 121.3100° W), Santa Clara (37.3600° N, 121.9700° W), and Santa Cruz (37.0300°N, 122.0100° W) (Fig. 1). The gardens range from 405 to 15,525 m² in size, are separated from one another by >2 km, and are surrounded by a mix of natural, agricultural, open green space, and impervious land cover (Fig. 1).

Aphid populations and parasitism

Due to its widespread abundance, its economic importance, and the presence of *Brassica* plants in all of our gardens, we chose cabbage aphids (*Brevicoryne brassicae*) as our model organism to examine local and landscape factors that affect herbivore regulation. Cabbage aphids are the most common and abundant aphid species on *Brassica* crops (e.g., cabbages, Brussels sprouts, kale) and, in urban agroecosystems, cabbage aphids infest crops and shorten crop life (Flint 2013). While other aphid species are present in the gardens (e.g., potato aphids (*Macrosiphum euphorbiae*), bean aphids

(*Aphis fabae*), green peach aphids (*Myzus persicae*)), cabbage aphids made up 99% of the individuals counted, and thus we decided to only focus on cabbage aphids for our study. Cabbage aphids are consumed by arthropod predators like ladybeetles and attacked by parasitoid wasps (Hymenoptera). Although ant-tending can deter predators and parasitoids (Müller & Godfray, 1999), in our study sites fewer than 2% of *Brassica* plants with cabbage aphids are tended by ants (Philpott S., unpublished data). While we have previously measured predation by other arthropods (e.g., spiders, ladybeetles, wasps) in this system (Philpott & Bichier, 2017), we have yet to measure the effect of parasitism on aphid regulation. Thus in this study we focused on parasitism of aphids.

The study gardens have abundant and diverse parasitoid wasp communities (Burks & Philpott, 2017). Parasitoids can provide significant pest control in urban ecosystems (Burkman & Gardiner, 2014), and are considered among the most important natural enemies of aphids in rural and urban agroecosystems (UC IPM, 2009, 2013). Parasitized aphids (i.e., "mummies") can be easily recognized by their leathery brown "bloated" bodies, and therefore easily quantified.

During the summer of 2016, we did monthly counts of cabbage aphid abundance and parasitism rates on *Brassica* plants in each garden (May 24–June 7, June 27–30, July 25–28, August 22–26). We visually surveyed cabbage aphids and aphid parasitism on five randomly chosen *Brassica* plants in five haphazard locations within a 20 × 20 m survey plot at the center of each garden. Different plants were sampled on the different sampling occasions. For each plant, we

counted the number of leaves, measured the plant height, and counted the number of non-parasitized and parasitized cabbage aphids. We used the University of California Agriculture and Natural Resources Integrated Pest Management Program's Guidelines to identify cabbage aphid individuals and colonies (UC IPM, 2009). We collected parasitized aphid mummies (n = 180) and reared them in the laboratory in plastic vials with a cotton stopper to identify parasitoid species for a qualitative assessment of natural enemies present. Parasitoids were identified to family using Naumann (1991, chap. 42). To measure parasitism rates we calculated a parasitism ratio following Roschewitz, Hücker, Tscharntke, and Thies (2005) (# mummies/(# aphids + # mummies)) and calculated host plant volume (number of leaves × plant height) for all *Brassica*.

Local and landscape factors

We collected data on garden environmental factors that we hypothesized directly and indirectly regulate aphid populations because they affect parasitoids in these gardens (Burks & Philpott, 2017; further described below). At two time points while sampling for aphids (late June and August 2016), we counted the number of *Brassica* plants within the 20 × 20 m plots for a measure of host plant density, and counted the number of flowers within eight random 1 × 1 m sub-plots within the 20 × 20 m plots because flowers are important nectar resources for parasitoids in agroecosystems (Balzan & Wäckers, 2013). We sampled soils for inorganic nitrogen content because increased nitrogen (N) increases plant phloem quality thereby potentially increasing the abundance of sap-sucking herbivores, such as aphids (Mattson, 1980; Nowak & Komor, 2010). We sampled soils rather than plant N because we did not have permission from all gardeners within the community gardens to remove plant material. We use soils as an indicator of plant N with recognition that these two metrics are not the same, but that plant N is often correlated with soil N in agroecosystems (Hofman & Van Cleemput, 2004). We sampled soils at the same five *Brassica* plants as the aphid surveys, taking three 0–20 cm soil cores within 10 cm of the plant's base with steel soil augers. We aggregated soil samples for one representative sample for each plant and performed a KCl extraction with fresh soil within 24 h following Wilke (2005). In addition, we sampled soils to determine soil water holding capacity (WHC), using a cylindrical metal sampler at four 1 × 1 m sub-plots per garden. Soil WHC is an indicator of soil fertility due to its influence on crop growth ability and is a standardized measure for indicating long-term water availability because it is less sensitive to sampling instance (i.e., when gardeners watered). Following Wilke (2005), we screened soils through a 2 mm sieve, filled a 2 × 2″ cylinder with a perforated base with field-moist soil, and submerged cylinders in a water bath for 8 h. We removed, capped cylinders (to avoid evaporation), and placed cylinders on a tray of sand. Once a consistent

weight of the soil sample was achieved over time, we dried the soil at 105 °C for 24 h.

We measured garden size (m^2) using Google Earth imagery (Google, 2016) because changes in habitat size may affect natural enemies and aphids in urban landscapes (Gibb & Hochuli, 2002). We used land cover data from the US Geological Survey's National Land Cover Database (NLCD) (Jin et al., 2013) to measure the proportion of urban developed land cover (determined by the amount of impervious or built cover) within buffers at a 1 km spatial scale surrounding each garden. We chose to focus on urban developed land because it may affect aphids and natural enemies by acting as a barrier to dispersal, and we selected 1 km because aphids and parasitoids respond to landscape factors at this spatial scale both in rural (Roschewitz et al., 2005; Gagic et al., 2011) and urban (Nelson & Forbes, 2014; Egerer, Arel et al., 2017) landscapes. Using spatial statistics tools in ArcGIS (v 10.1) (ESRI, 2011), zonal histograms identified the total proportion cover of three NLCD land cover classes present within each buffer that represent urban land cover (Homer et al., 2015): (1) low density housing land cover (49% impervious cover; land cover class # 22), (2) medium density housing land cover (50–79%; # 23), and (3) high density housing and buildings (80–100%; # 24). We combined the three classes for a total proportion of urban land cover surrounding gardens at 1 km. Here, a high total proportion of urban land cover indicates higher degrees of urbanization, and a low proportion indicates low degrees of urbanization.

Analysis

We used generalized linear models to compare aphid density and parasitism ratios among counties and across sampling period. The number of aphids observed and the calculated parasitism ratio per *Brassica* survey were the response variables, and county and sampling period were the predictors. The aphid density model was fit with a Poisson distribution and the parasitism model was fit with a negative binomial distribution. We fit the full model and ran a post-hoc test using the *glht* function in the *multcomp* package (Hothorn, Bretz, & Westfall, 2008) in the R statistical environment (R Development Core Team, 2016) to assess differences between counties and sampling periods. Second, we constructed a conceptual path analysis model, a form of structural equation modeling (SEM) (Mitchell, 2001), to understand the relative importance of direct and indirect effects on aphid density using a priori knowledge of the local and landscape factors that affect parasitoid abundance, species richness, and species composition in the same gardens (see Burks & Philpott, 2017) (Fig. 2). In the model, we predicted that host plant size and density (*sensu* the *resource concentration hypothesis*), and proportion of urban land cover would positively directly affect herbivore density (Newman, 2003; Turrini et al., 2016). We also predicted that soil properties (WHC, inorganic nitrogen (NO$_3^-$) concentra-

Table 1. Overview of the minimum, maximum, mean (±standard error of the mean) values of the local management factors averaged per site across all 25 garden sites at the two time periods measured.

	June			August		
	Min	Max	Mean ± SE	Min	Max	Mean ± SE
Aphid density (avg. plant)	14	82	42 ± 3	1	65	31 ± 3
Parasitism (ratio)	0.04	0.50	0.24 ± 0.02	0.20	0.82	0.37 ± 0.03
Floral density (1 × 1 m)	1	1328	192 ± 56	1	470	48 ± 21
Brassica density (20 × 20 m)	2	371	55 ± 16	4	262	41 ± 12
Host plant volume[a]	4.3	9.2	6.7 ± 0.1	4.5	8.5	6.6 ± 0.1
Soil inorganic N (mg/kg soil)	0.1	8.2	1.5 ± 0.4	0.1	13.2	2.4 ± 0.6

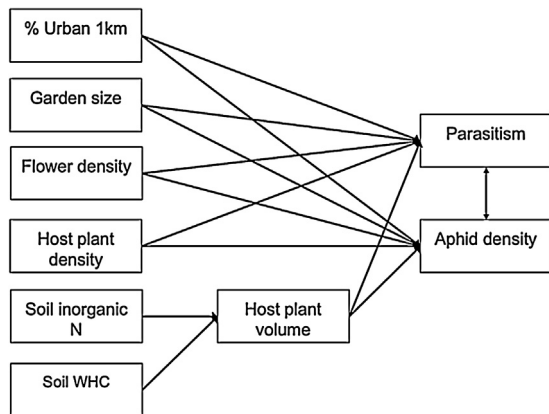[a] Average plant height multiplied by the number of leaves, natural log transformed.

Fig. 2. Conceptual path analysis model of direct and indirect effects on aphid density and parasitism.

tion) would positively indirectly affect herbivore density by directly affecting plant size and quality (*sensu* the *plant stress hypothesis*). Moreover, we predicted that garden size and floral abundance (density) would positively directly affect parasitism (*sensu* the *enemies hypothesis*), while the proportion of urban land cover would negatively directly affect parasitism to indirectly affect herbivore density through a connection between parasitism and herbivore density (i.e., via trophic cascade). Last, we predicted that effects would change over the season due to fluctuations in populations and thus trophic interactions throughout the growing season in response to changes in environmental factors and agricultural management.

We built the SEM with generalized linear mixed effects models using piecewiseSEM (Lefcheck, 2016) in R. This approach (1) accounted for the hierarchical structure of the data (*Brassica* nested within site, nested within counties), (2) allowed for the incorporation of random effects (site nested within county) and (3) accepted flexible response variable distributions. For each mixed effects component model, we added a random effect. The aphid density component model was fit with a Poisson distribution, the parasitism model was fit with a negative binomial distribution, and the host plant volume model was fit with a Gaussian distribution. Explanatory variables were the averaged local factors

measured at each respective sampling period for each site with the exception of soil WHC, proportion of urban land cover, and garden size, which we assumed did not change significantly across the season and thus were collected once per year. Explanatory variables were standardized and centered prior to analysis. To examine whether patterns change over time, we built two SEMs to analyze early growing season pathways (late June) and later growing season pathways (August) (see Table 1 for how variables differ by month). For each model we obtained standardized regression coefficients using the *sem.coefs* function and model fit tests using the *sem.model.fits* function. Here, good model fits are determined by a Fisher's C statistic calculated by the significance of all missing paths (Shipley, 2009), a X^2 test (the model is an adequate fit when $P > 0.05$), and Akaike's information criterion (AICc) value (Lefcheck, 2016).

Results

Trends in aphid density and parasitism

Cabbage aphid density, but not parasitism, on *Brassica* significantly varied in gardens across counties and sampling periods (Fig. 3; Table 2). Santa Cruz gardens had significantly lower aphid densities than Monterey ($P < 0.001$) but greater aphid densities than Santa Clara ($P = 0.01$), whereas Monterey and Santa Clara gardens significantly differed from one another ($P < 0.001$; Fig. 3A; Table 2A). Cabbage aphid densities significantly differed in late June ($P < 0.001$) and July ($P < 0.001$) from May, but not in August ($P = 0.147$; Table 2A). Parasitism on *Brassica* generally declined from May to July across sites among counties, but then increased in August (Fig. 3B; Table 2B). Mean parasitism per site ranged from 0% parasitism in May to up to 26% in August (Table 1). Of the 180 reared aphid mummies, 33 parasitoids emerged (18.3%), consistent with low rearing success in other studies (van Veen, Morris, & Godfray, 2006). The identified parasitoid families that emerged from collected cabbage aphid mummies were Pteromalidae (36.4%; n = 12 individuals), Braconidae (30.3%; n = 10), and Figititdae (27.3%; n = 9). To note, Braconidae species are primary aphid parasitoids,
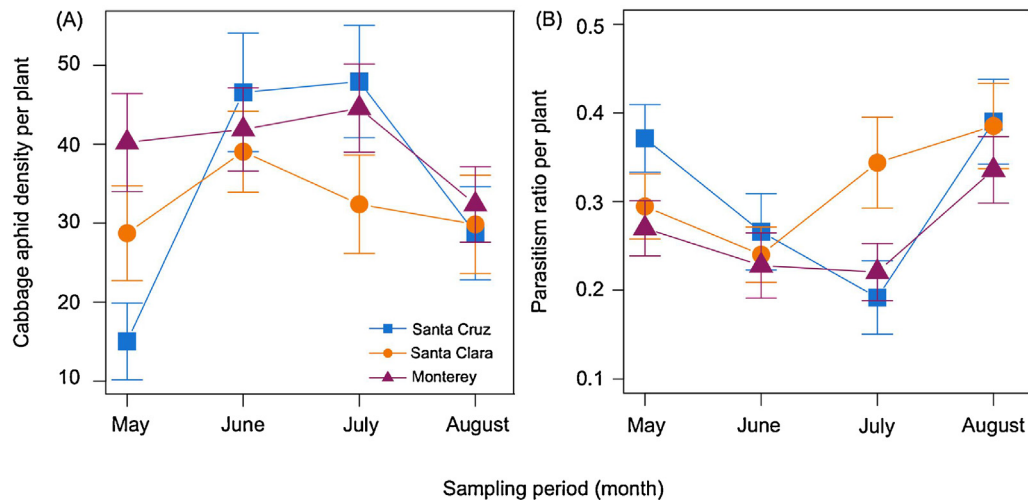
Fig. 3. Trends in (A) cabbage aphid density and (B) cabbage aphid parasitism (ratio) across counties and across sampling periods. Symbols in the plots represent the mean value (density, parasitism) for the gardens for each county. Error bars represent standard errors (SE) of the means.

Table 2. Analysis of (A) cabbage aphid density and (B) parasitism using generalized linear regression models. Parameters indicate the counties in which the community gardens are located (Santa Cruz county as reference level), and the sampling period (month) (May as reference level). Significant differences among counties and months assessed through post-hoc comparisons indicated with superscripts.

	Parameter	Coefficient	SE	z	P
A. Aphid density	County				
	Intercept (Santa Cruz)[a]	3.54	0.01	246.47	<0.001
	Santa Clara[b]	−0.06	0.02	−2.91	0.004
	Monterey[c]	0.14	0.02	7.70	<0.001
	Sampling period				
	Intercept (May)[a]	3.38	0.02	202.27	<0.001
	June[b]	0.36	0.02	16.54	<0.001
	July[b]	0.35	0.02	15.93	<0.001
	August[a]	0.03	0.02	1.45	0.147
B. Parasitism	County				
	Intercept (Santa Cruz)[a]	−0.82	0.15	−7.76	<0.001
	Santa Clara[a]	0.04	0.21	0.17	0.865
	Monterey[a]	−0.15	0.21	−0.71	0.481
	Sampling period				
	Intercept (May)[a]	−0.82	0.16	−7.20	<0.001
	June[a]	−0.23	0.25	−0.94	0.345
	July[a]	−0.20	0.24	−0.82	0.410
	August[a]	0.18	0.22	0.81	0.419

ovipositing directly inside of the aphid that leads to permanent aphid paralysis and mummification (Stary, 1970). Many species of Pteromalidae (Superfamily: Chalcidoidea) and Figititdae (Cynipoidea) are secondary parasitoids, or hyperparasitoids, that attack aphids but delay development until aphid mummification by the primary parasitoid occurs (Müller, Adriaanse, Belshaw, & Godfray, 1999).

Direct and indirect effects

The conceptual SEM had predictive power of the direct and indirect effects of local and landscape factors on aphid density and parasitism across the season (June: Fisher's $C_{12} = 14.13$, P = 0.29, AICc = 81.26; August $C_{12} = 6.14$, P = 0.91, AICc = 70.27) with a higher model fit in August. Cabbage aphid density was significantly negatively correlated to parasitism over the season, both in June and August (coefficients listed in Fig. 4, see Supplementary Appendix A: Table 1; Fig. 1). Local factors directly affected cabbage aphid density but their importance varied between seasonal time points. Floral density significantly negatively affected June cabbage aphid densities (P = 0.005), host plant density positively affected August aphid densities (P = 0.009), and host plant volume had a significantly positive effect on aphid
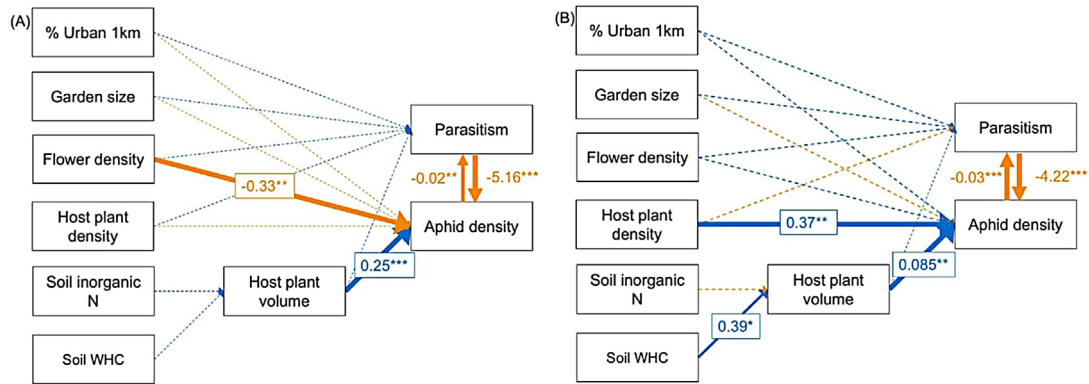
Fig. 4. Path diagrams of garden trophic interactions for (A) June and (B) August displaying standardized coefficients of effects. Line type (solid vs dashed) indicates statistically significant effects (solid lines; $* = P < 0.05$, $** = P < 0.01$, $*** = P < 0.001$; dashed lines insignificant). Blue lines indicate positive effects; orange lines indicate negative effects. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

densities in both June ($P < 0.001$) and August ($P = 0.004$) (Fig. 4A; see Supplementary Appendix A: Table 1). Soil water holding capacity had a significant positive effect on host plant volume in August ($P = 0.01$), indirectly affecting aphid densities (Fig. 4B). Local factors only indirectly affected parasitism across the season through the connection between aphid density and parasitism. The landscape factor (urban land cover) did not have significant effects on either aphid density or parasitism.

Discussion

We found strong evidence of local garden management factors directly and indirectly affecting herbivore populations. We also found a strong negative correlation between parasitism ratios and cabbage aphid population density. Contrary to expectations, we did not find any significant effects of the amount of urban land cover in the landscape on aphid densities nor on parasitism. Furthermore, none of the predicted factors had any direct effects on parasitism. The relative importance of the effect of management varied temporally as indicated by a higher fit of the August model, and the significant differences in aphid densities over time. Consequently, we focus on interpreting the August model in the following discussion.

Influence of garden management factors on herbivores

A soil management factor, water holding capacity (WHC), directly increased host plant volume, to have positive indirect effects on aphid densities. High soil WHC is associated with more soil organic matter and improved soil fertility through soil and groundcover amendments in these gardens (Egerer, Philpott et al., 2017). Such management practices (e.g., composting) have been shown to reduce plant water stress and

enhance plant growth, which can then lead to aphid population growth (Archer, Bynum, Onken, & Wendt, 1995). Garden soils with higher WHC retain moisture for longer to prevent water stress – especially later in the season – and thereby can support host plant growth to ultimately support more herbivores. These findings follow predictions that host plant condition matters for herbivores, in particular that larger host plants can support higher aphid densities (Dixon, 1977).

Our results suggest that nitrogen availability in the soil may not be as important as plant water content for aphid populations in these gardens. The fact that plant turgor pressure and cell water content is necessary for phloem feeders' nitrogen utilization (Huberty & Denno, 2004) could explain why we found no direct effect of soil inorganic nitrogen on host plant volume or no indirect effect on aphid density. Our findings could also mean that either this measure of plant condition was too coarse, that plant quality may be relatively similar in gardens (particularly in relation to outside garden vegetation), or that fertilization may not universally increase herbivore population loads in urban systems (Dyer & Stireman, 2003).

In accordance to the *resource concentration hypothesis* (Root, 1973), we found that greater host plant densities resulted in greater aphid densities in the gardens. These results concur with studies in rural agricultural systems (Andow, 1991), in urban home gardens (Shrewsbury & Raupp, 2006), and other green space patches (Fenoglio et al., 2009). Greater *Brassica* density across the garden habitat provided an abundant resource for aphid populations to exploit, as well as shorter travel distance between host plants. Decreasing proximity between plants, often associated with higher plant density, likely facilitates herbivore movement from and colonization to new host plants (Hambäck, Björkman, Rämert, & Hopkins, 2009) and is particularly important for herbivores like aphids that reproduce quickly and disperse with increasing colony density on plants (Dixon, 1977). Since increasing herbivore density increases the likelihood of plant damage (Kim & Underwood, 2015), it

would be valuable to further examine the maximum density of conspecific plants in a garden before increases in damaging herbivore populations occurs.

Influence of garden management factors on herbivore-parasitoid interactions

The strong negative relationship between aphid density and parasitism suggests that parasitoids can regulate herbivore populations through top-down pathways. Although parasitism was not as high at high aphid densities, even ∼30% parasitism may be sufficient to keep aphid densities from increasing further. Surprisingly, none of the local or landscape drivers had direct effects on parasitism, meaning that parasitism is driven by the availability of herbivore hosts but not necessarily garden management factors. In particular, the number of flowers within gardens directly negatively affected aphid densities, but counter to our predictions did not directly affect parasitism. This contrasts with previous studies of parasitism in rural agricultural systems where parasitism increases with agroecosystem floral availability (Jonsson, Wratten, Landis, Tompkins, & Cullen, 2010), but supports other findings that local factors including floral availability have no direct effect on parasitism in urban systems (Hanks & Denno, 1993; Dale & Frank, 2014; Lowenstein, Gharehaghaji, & Wise, 2017). Flowers may, however, instead attract other aphidophagous predators that are negatively affecting aphid densities. Indeed, ornamental flowers increase ladybeetle abundance in our system (Egerer, Bichier, & Philpott, 2017), and syrphids, whose larvae predate aphids, are generally supported by floral resources in agroecosystems (Landis, Wratten, & Gurr, 2000; Haenke, Scheid, Schaefer, Tscharntke, & Thies, 2009). While here we focus on the role of parasitism for herbivore regulation, we acknowledge that other predators could reduce aphid densities and influence parasitism ratios by altering the density and spatial distribution of prey, or by consuming parasitized individuals to skew observations. Aphid-tending ants could potentially affect aphid densities (Müller & Godfray, 1999), but the few observations (2%) of *Brassica* with ants in these gardens (as described above) suggest that ants are not playing a strong role in inhibiting *Brassica* parasitoids in these gardens.

Other local vegetation characteristics not measured here may be important drivers of parasitism. A recent study found that not only host plant species diversity but greater plant phylogenetic diversity may be important for decreasing herbivore densities and increasing parasitism by providing more microhabitats and microclimates within habitats to support parasitoid communities (Staab et al., 2016). Therefore, incorporating plant structural diversity (e.g., reducing concentrations of host plants in plots) and phylogenetic diversity (e.g., increasing the number of cultivated varieties of host plants) in urban gardens may be important for increasing parasitoid abundance and diversity to thereby increase parasitism.

Influence of urban context on herbivore-parasitoid interactions

The proportion of urban cover in the landscape did not directly or indirectly affect aphid densities or parasitism in the studied community gardens. Herbivores like aphids may be less susceptible to landscape-scale urban environmental disturbances due to relatively high local host plant abundance and quality within gardens compared to the surrounding environment. Here, gardens provide an irrigated and productive habitat with more resources during drought conditions (Faeth et al., 2005) like in California during this study, and could influence aphid densities. Aphids can also disperse relatively long distances to locate habitat patches as they are carried by wind currents (Compton, 2002), and this passive long-distance dispersal ability may be why aphid densities are unaffected by changes in the amounts of impervious cover in the landscape. Although parasitoids are generally more sensitive to land use intensification (Tscharntke & Brandl, 2004) like urbanization (Denys & Schmidt, 1998), our findings are comparable to other urban studies that found no strong effects of urbanization on variation in herbivore parasitism (Fenoglio et al., 2009; Bennett & Gratton, 2012b; Lowenstein et al., 2017). This previous work suggests that some parasitoid species may be more tolerant of anthropogenic disturbance, particularly those that are efficient natural enemies, to maintain similar levels of pest control across gradients in landscape-scale urbanization (Fenoglio et al., 2009).

Temporal variation in herbivore regulation, herbivore-parasitoid interactions

The relative importance of direct and indirect local effects changes over the season, as indicated by the difference in model fit between months and the relative effect of local variables. This may be attributed to the observed fluctuations and variability in aphid densities across sampling periods across counties. Yet, while aphid densities fluctuated across the season, across counties, and with changing management factors, parasitism did not differ over time despite these fluctuations in their hosts. This suggests that although parasitoid communities are linked to aphid densities, they are likely limited in their ability to regulate herbivores at high densities. The differences in responses over the season could further be explained by abiotic factors that we did not directly measure, such as increasing urban temperatures that can boost herbivore fitness on host plants without affecting herbivore regulation by natural enemies (Dale & Hanks, 2014).

Conclusions

Population dynamics and trophic interactions are modified in urban agroecosystems through human land management at local and landscape scales. In community gardens, aphid herbivore pest population regulation can be driven by direct effects (through vegetation properties) and indirect effects (through soil properties) on herbivores predominantly through bottom-up pathways. Moreover, local management of soil and vegetation within gardens was here more important for aphid pest control than the degree of urbanization surrounding gardens. This suggests that gardeners can, to some degree, regulate aphid populations through vegetation and soil management. Vegetation structure and composition, particularly of *Brassica* crops that are favorites of both gardeners and aphid herbivores, may be strategically planned or intercropped within garden beds and across the garden habitat to lower aphid densities. Further, interspersing flowering plants or diversifying the crops planted may reduce aphid densities as well. Changes in soil management, however, may not benefit gardeners due to important agroecosystems trade-offs. On the one hand, building soil organic matter through composting or mulching may increase soil water holding capacity, boost plant growth, and conserve water in urban agroecosystems (Edmondson, Davies, Gaston, & Leake, 2014), but our findings suggest that related increases in plant quality may boost aphid populations, without increases in parasitism. In order to maintain high plant quality, while also managing pests, gardeners should carefully monitor herbivore populations, and follow other general recommendations for supporting parasitoid and natural enemy populations within gardens (Shrewsbury, Lashomb, Patts, & Casagrande, 2004; Raupp et al., 2010; Flint, 2013). In sum, agroecosystem management should recognize and balance the trade-offs that result from the concert of direct and indirect effects in agroecosystem pathways to ultimately enhance pest control services.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2018.02.006.

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