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## AGROECOSYSTEMS

# Plant damage in urban agroecosystems varies with local and landscape factors

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**Abstract.** Biotic and abiotic factors at local to landscape scales influence insect pest and disease dynamics in agricultural systems. However, relative to studies focused on the importance of these drivers of crop plant damage in rural agricultural systems, few studies investigate plant damage from herbivore insects and plant diseases in urban agroecosystems, and consequently, most urban farmers lack knowledge on crop protection tactics. Here we use three common crop species within urban agroecosystems (community gardens) distributed across an urban landscape as a model system to ask how local, landscape, and microclimate factors relate to herbivore and disease plant damage. We hypothesized that plant damage would be lower in gardens with greater local vegetation complexity, landscape-scale complexity, and less variable temperatures, but that the importance of factors is species- and damage-specific. By measuring *Brassica*, cucurbit, and tomato insect pest and disease damage across the growing season, we confirmed that the importance of factors varies with crop species and by damage type. Both local complexity factors (e.g., number of trees and shrubs) and landscape complexity (percent natural cover in the landscape) relate to lower incidence of herbivore and disease damage on some crops, supporting our prediction that habitat heterogeneity at both local and landscape scales lowers plant damage. Greater temperature variability related to higher disease damage on tomatoes linking microclimate factors to disease prevalence. Yet, local complexity factors also related to higher incidence of plant damage for other crop species, indicating variable species-level impacts of local management factors on plant damage. By measuring the abundance of fungus-feeding lady beetles (*Psyllobora*) on cucurbits, we confirmed a strong association between natural enemies and powdery mildew. We provide a case study on how changes in local to landscape-scale factors relate to plant damage in urban agroecosystems and suggest how urban farmers and gardeners can apply this ecological knowledge to improve sustainable urban food production.

**Key words:** agroecological management; California; conservation biological control; disease; herbivory; temperature variability; urban agriculture.

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## INTRODUCTION

In agricultural systems, farmers are continuously challenged by a wide range of crop-

damaging pests. Insect, bacterial, and fungal agricultural pests cause billions of dollars of crop damage annually (Losey and Vaughan 2006). Both biotic and abiotic factors affect the bottom-

up and top-down forces that drive pest control in agroecosystems (Thies and Tscharrntke 1999, Gonthier et al. 2013, Liere et al. 2015). Agroecological practices aimed at preventing insect herbivore and plant disease outbreaks include crop diversification and rotation (Altieri 2004, Bommarco et al. 2013). Ecological principles based in biological diversification, closed-loop cycling, species interactions, and spatio-temporal complexity underlie these practices. On the one hand, as predicted by the enemies hypothesis, increasing habitat heterogeneity—by diversifying crop composition and structure, and adding floral resources—leads to increased natural enemy abundance and diversity, thereby enhancing crop pest suppression (Root 1973). On the other hand, the resource concentration hypothesis predicts that higher concentrations of host plants and less vegetation diversity facilitate host plant location ultimately leading to herbivore and disease outbreaks. Both of these hypotheses support the idea that local habitat heterogeneity reduces herbivore and disease outbreak both through herbivore and disease resource manipulation, and through increased herbivore and pathogen mortality by natural enemies to enhance pest control (Kremen and Miles 2012, Rusch et al. 2013, Marja et al. 2018). Agroecological practices grounded in ecological theory have potential to minimize crop plant damage and enhance crop production through on-farm management of habitat structure (Garibaldi et al. 2018), but further studies are needed.

In addition to local agroecosystem features at the farm scale (Batáry et al. 2011), the effect of agroecosystem management on biodiversity and ecosystem function largely depends on landscape context (Tscharrntke et al. 2005). In systems embedded within simplified landscapes with less natural habitat, agroecological management has larger, positive effects on biodiversity and ecosystem functions than in systems in more complex landscapes with more natural habitat to an extent, though the relationship is not linear. Along with effects on herbivores and natural enemies, landscape context may also influence epidemic invasions and plant disease spread in agricultural systems through habitat connectivity (Mundt et al. 2011). Many crop diseases including fungal pathogens and air-borne diseases are capable of long-distance aerial dispersal (e.g., via

spores) across the landscape (Brown and Hovmøller 2002). Consequently, the disease prevalence and disease dynamics within an agroecosystem may largely depend on surrounding landscape composition through dispersal facilitation or limitation (Plantegenest et al. 2007). Yet, the epidemiology of crop diseases and the influence of landscape complexity on disease spread are still largely unknown. Furthermore, though increased heterogeneity in the landscape generally increases natural enemy diversity, the effects on crop pest suppression are highly variable (Karp et al. 2018).

Organisms within agricultural landscapes and crop susceptibility to herbivores and disease are also inevitably affected by climate features of the environment. For crops, temperature variability and exposure to extreme heat and drought influence plant physiology, growth, development, and yield (Prasad et al. 2008, Asseng et al. 2011). Temperature also facilitates the spread and severity of crop diseases and pathogens through effects on disease occurrence and development (Colhoun 1973). Extreme temperature fluctuations can weaken plant defenses to herbivores and disease (Mattson and Haack 1987, Luck et al. 2011, Raffa et al. 2013), impact fruit quality, and increase the likelihood of crop failure (Teixeira et al. 2013). Increased temperature variability under climate change is consequently forecasted to reduce crop yield (Fuhrer 2003, Tubiello et al. 2007, Deutsch et al. 2018). Some diseases are associated with elevated temperatures, and other diseases are associated with low temperatures, meaning that temperature variability impacts pathogen survival and fitness. Thus, assessing local temperature variability is necessary to understand how abiotic factors affect crop plant damage and ultimately sustainable food production.

Conservation biological control is a habitat management strategy in agroecological farm design that implements ecological knowledge of local and landscape biotic and abiotic factors to promote pest (insect, disease) suppression. Farm managers utilize knowledge of ecological principles such as biological diversification, structural complexity, and species interactions to reduce crop exposure and vulnerability to pests through intrinsic crop protection by natural enemies and associated resistance (Heimpel and Mills 2017). At the local farm scale, conservation biological

control practices include incorporating non-crop perennials, floral resources, and agroforestry (Rusch et al. 2013, Crowder and Jabbour 2014). At the landscape scale, natural vegetation and non-crop land surrounding farms are linked to insect pest (Tscharntke et al. 2005, 2007, Gardiner et al. 2009, Martin et al. 2019) and disease regulation through greater landscape complexity (Plantegenest et al. 2007). Thus, both local to landscape-scale management that incorporates conservation biological control ideas and practices can provide ecologically based interventions to reduce crop plant damage and boost yield.

Urban agroecosystems, including urban farms and gardens, vary greatly in vegetation management and urban landscape context, and are often managed at a much smaller spatial scale than rural farms, meaning that management strategies should be very different (Tiffany 2017). Compared to rural agroecosystems, little is known about crop pests in urban agriculture (Surls et al. 2014). This is problematic because over 60% of urban farmers report pest-related challenges (Oberholtzer et al. 2014) and sustainable pest management is highly knowledge- and time-intensive (Gregory et al. 2015). Consequently, research-informed pest management training and educational materials for urban agriculture are needed (Surls et al. 2014). Unique biotic and abiotic characteristics of cities alter bottom-up and top-down forces with potential consequences for herbivore and disease regulation. For example, irrigation and plant fertilization can increase host plant quality, benefitting herbivore populations (Faeth et al. 2005), while warmer temperatures due to urban heat islands increase herbivore fecundity and pathogen spread, lowering effectiveness of natural enemies (Raupp et al. 2010, Dale and Frank 2014). Natural enemies, which depend on natural areas for alternative resources and overwintering sites (Landis et al. 2000), are often negatively affected by urbanization (Fenoglio et al. 2013), and urban temperature extremes can reduce top-down regulation (Meineke et al. 2014). However, the combined effects of changes in microclimate, local vegetation management, and landscape context on crop pests, natural enemies, and crop plant damage in urban agroecosystems remain unclear. This information is crucial given the limited set of pest control options (e.g., non-chemical) and fewer

grower support and resources (e.g., the Cooperative Extension Service) designed for urban agriculture (Reynolds 2011, Surls et al. 2014).

In this study, we aimed to improve our ecological understanding of the local and landscape factors affecting crop plant damage in urban agroecosystems across an urban landscape in California, USA. We specifically examined the effects of local vegetation management, local temperature variability, and surrounding landscape context on crop plant damage by insect herbivores and disease. To do so, we used three common crops in urban agroecosystems as a model system to ask how these local and landscape factors relate to different types of common plant damage by herbivores and disease over the growing season. We asked: (1) How do local agroecosystem vegetation management factors, local temperature variability, and landscape context (the amount of natural habitat in the surrounding landscape) affect plant damage on cole crops (*Brassica oleraceae*), cucurbits, and tomatoes? Is there an interaction between local and landscape factors? (2) Do these factors differentially affect herbivore versus disease plant damage? We tested the hypotheses: (1) Plant damage will be lower in more vegetatively heterogeneous urban agroecosystems than in homogeneous ones; (2) plant damage will be lower when the agroecosystems are embedded in more complex urban landscapes with greater amounts of natural habitat land cover; (3) there will be an interaction between local and landscape effects (i.e., the effect of local factors will depend on landscape context), where the positive effects of local factors will be higher in less complex landscapes with less natural cover; (4) plant damage will be lower in urban agroecosystems with less variable temperatures due to less exposure to temperature extremes; and (5) the effects of local vegetation, temperature, and landscape factors vary with herbivore versus disease damage.

## METHODS

### *Study system*

We worked in 24 urban community gardens (henceforth “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; Appendix S1: Fig. S1). The gardens ranged from 405 to 15,525 m<sup>2</sup> in size, were separated from one another by >2 km, and were surrounded by a mix of natural (e.g., forest, grass, shrub), agricultural (e.g., crop, pasture), open green space (e.g., parks, golf courses), and urban impervious land cover (Egerer et al. 2017a). We chose gardens that varied both in surrounding landscape factors and in local management factors (e.g., vegetation composition and structure, ground cover). All gardens are managed toward the cultivation of organic produce; however, agricultural practices and pest management strategies (e.g., hand removal and biologically based products) differ between gardens and may influence our results. Within each garden, we concentrated sample efforts within a 20 × 20 m plot at the center of each garden. We sampled gardens at three sampling periods across the growing season (June 25–28, July 16–19, August 6–9, 2018).

**Plant damage**

We studied plant damage from herbivores and diseases on three common crop plant species in our study system: cole crops (*Brassica oleracea*; henceforth "*Brassica*"), cucurbits (squash, cucumber, melons; *Cucurbita pepo*), and tomato (*Solanum lycopersicum*). We chose three different crop species as a model system because they are common crops found in all gardens and experience different forms of plant damage. We measured plant damage using crop-specific techniques (Table 1). At each of the three sampling periods, we randomly selected individuals of each of the focal crop species in each garden ( $n = 20$  cole

crop individuals;  $n = 3$  cucurbits;  $n = 3$  tomatoes). The sampled plants were not the same across all three sampling periods, and sample size varied with plant availability at a site. In addition, the presence of crop varieties varied across the site, meaning that we could not control sampling for varietal differences. Therefore, all analyses consider crop species, regardless of variety. For *Brassica*, we randomly selected two leaves per plant (top, bottom) and using a transparency film with a 2 × 2 cm grid counted (1) squares with damage from chewing, sucking, and mining herbivore insects and (2) squares with disease damage (identifying the disease if possible). We also measured the plant height and width. For cucurbits, we counted (1) leaves with and without powdery mildew and (2) fruits with and without mildew, sun, or herbivore (mammal) damage. For tomatoes, we counted fruits with and without disease, sun, or herbivore (bird) damage. We also collected data on the total number of healthy and damaged tomato and cucurbit plants in the 20 × 20 m plot (e.g., garden scale in Table 1) to assess disease damage from tomato wilt and powdery mildew. We counted the number of all *Brassica*, cucurbit, and tomato plants within the 20 × 20 m plot as a measure of conspecific density.

On each sampled cucurbit plant, we recorded the presence of *Psyllobora vigintimaculata*—a fungus eating lady beetle natural enemy. We did this because previous investigations suggested that this species is associated with mildew on plants and could be providing disease regulation (Egerer et al. 2016). Thus, this measurement was designed to obtain a quick assessment of natural

Table 1. The three focal crop species in this study and their common forms of plant damage, both leaves and fruits, sampled in this study and the sampling effort for each crop.

Focal crop	Leaf damage	Fruit damage	Sampling effort
Cole crop ( <i>Brassica</i> )	Herbivory (insect): chewing, sucking, mining herbivory Bacterial and fungal disease: leaf spot, rot, mildew, rust	NA	20 plants × 3 sampling periods = 60/site
Cucurbit	Powdery mildew Chewing herbivory (insect) Herbivory (mammal)	Sun scorch Mildew	(a) 3 plants × 3 sampling periods = 9/site (b) Diseased vs healthy in site (20 m <sup>2</sup> ) × 3 sampling periods
Tomato	Tomato wilt ( <i>Fusarium</i> and <i>Verticillium</i> wilt) Herbivory (bird) Disease	Sun scorch Mildew	(a) 3 plants × 3 sampling periods = 9/site (b) Diseased vs healthy in site (20 m <sup>2</sup> ) × 3 sampling periods



enemy presence in relation to mildew abundance to inform potential pest regulation by natural enemies on a crop plant.

**Local vegetation management, temperature, and landscape factors**

Within each garden, we collected information on local vegetation and ground cover, temperature, and the amount of natural habitat cover in the surrounding landscape as hypothesized factors that affect plant damage (Table 2; Fig. 1). For local vegetation management factors, we measured local vegetation and ground cover factors at each sampling period. In each garden, within the 20 × 20 m sampling plot, we randomly placed eight 1 × 1 m quadrats within which we identified all herbaceous plants (except grasses) to morphospecies, counted all flowers, and assessed percent ground cover of mulch woodchips (a common ground cover

amendment used to suppress weedy vegetation). We counted and identified all trees and shrubs in the garden. In addition, we estimated the total garden size (m<sup>2</sup>) using Google Earth imagery because agroecosystem size can considerably affect communities of insects and plants.

For the local temperature factor, we measured the variability in temperature within each garden with a temperature logger (Onset HOBO UA-001-08; 5.8 × 3.3 × 2.3 cm in size, 8 K in Memory; www.onsetcomp.com/products/data-loggers/ua-001-08). The loggers have an operating range of -2°–70°C, an accuracy of ±0.53°C within 0°–50°C, and a temperature resolution of 0.14°C at 25°C. Three weeks prior to the first sampling period, temperature loggers were placed 1.3 m above the ground in the center of the garden and set to record hourly averaged ambient temperature measurements. Temperature loggers were protected from ultraviolet radiation with

Table 2. Descriptive statistics for the (a) local and landscape factors measured across the gardens across the sampling period hypothesized to predict plant damage and (b) the plant damage measurements observed across sampled plants, at each respective scale, in the gardens across the sampling period (b).

Variable	Mean	SD	Min	Max
<b>(a) Local and landscape predictor variables</b>				
Garden size (acres)	1.1	0.9	0.1	3.8
Temperature variability (temp. SD)	6.3	1.4	3.2	8.9
Arboreal abundance (No. trees and shrubs)	21.5	18.3	0.0	73.0
Vegetation complexity (No. herbaceous plant species)	22.0	6.0	7.0	39.0
Floral abundance (No. flowers within 1 m <sup>2</sup> )	88.5	152.1	3.8	833.5
Ground cover (% woodchip mulch ground cover within 1 m <sup>2</sup> )	20.6	18.1	0.0	90.4
Landscape complexity (No. natural land cover; 2 km)	13.9	19.7	0.0	61.2
Conspecific density (No. <i>Brassica</i> )	41.5	49.2	1.0	220.0
<b>(b) Plant damage response variables</b>				
<i>Brassica</i>				
Chewing damage (% leaf area)	11.1	15.4	0.0	35.0
Sucking damage (% leaf area)	11.4	17.3	0.0	55.0
Mining damage (% leaf area)	0.6	3.3	0.0	7.0
Disease damage (% leaf area)	4.3	12.0	0.0	50.0
Total damage (% leaf area)	26.9	24.4	0.0	101.0
<i>Cucurbit</i>				
Mildew prevalence within garden (% of plants)	34.0	28.0	0.0	100.0
Fruit herbivory (% No. fruits)	1.0	5.0	0.0	33.0
Fruit sun damage (% No. fruits)	4.0	16.0	0.0	100.0
Fruit mildew damage (% No. fruits)	1.0	4.0	0.0	22.0
Leaves with mildew (No. leaves)	11.3	8.8	0.0	37.7
<i>Tomato</i>				
Wilt prevalence within garden (% of plants)	22.4	23.1	0.0	87.0
Fruit herbivory (% No. fruits)	2.0	3.0	0.0	10.0
Fruit sun damage (% No. fruits)	0.0	1.0	0.0	7.0
Fruit disease damage (% No. fruits)	1.0	4.0	0.0	26.0

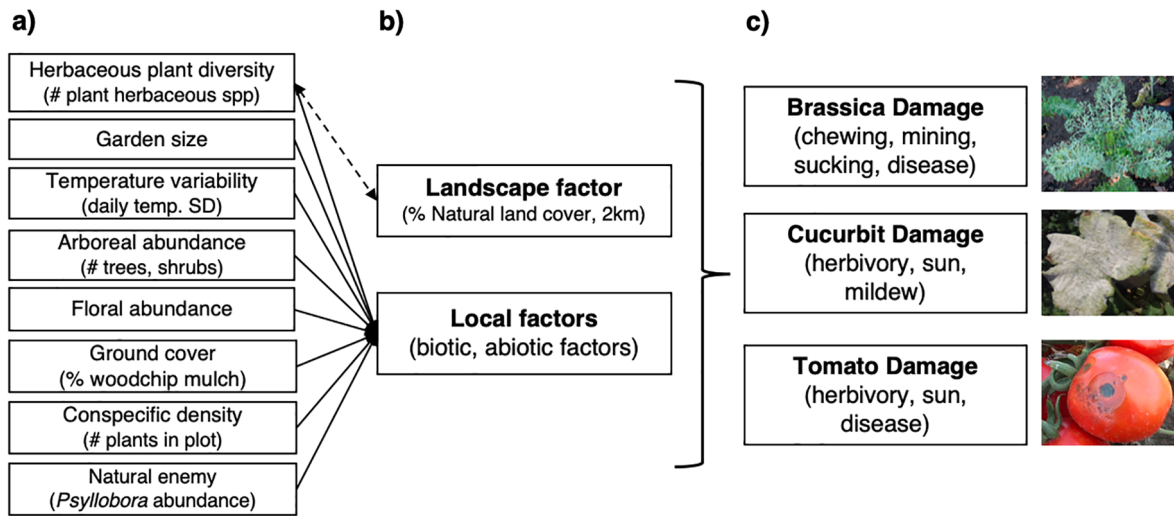


Fig. 1. Measured local vegetation and temperature factors in the gardens (a) and a landscape factor (b) that represent the predicted effects of local and landscape factors on observed plant damage of leaves and fruits for three common crops (c) in urban agroecosystems (community gardens). Dashed line connecting herbaceous plant species diversity and the amount of natural habitat land cover within 2 km in the landscape represents the interaction between local and landscape factors tested in the model. Images courtesy of the University of California Integrated Pest Management Program (<http://www.ipm.ucanr.edu>; Copyright © 2020 Regents of the University of California; licensed under the Creative Commons Attribution-NonCommercial-No Derivatives 4.0 International License).

white plastic shields fastened over them and checked throughout the survey period to ensure no radiation error (Terando et al. 2017). We downloaded and collected the data at the end of the study using an Optic USB interface, and quality checked and cleaned the data. We calculated interday variation in daily mean temperature for each garden for each sampling period (i.e., over the three weeks prior to field sampling) based on standard deviation (SD). This measure of fine spatial and temporal scale temperature variability was used as explanatory factor for predicting differences in plant damage.

For the landscape factor, we used land cover data from the US Geological Survey’s National Land Cover Database (NLCD; Jin et al. 2013) at 30-m spatial resolution to measure the proportion of natural and semi-natural land cover (henceforth natural land cover for simplicity) within buffers at a 2-km spatial scale surrounding each garden. We define natural land cover to be the total of deciduous (NLCD number 41), evergreen (42), and mixed forests (43), dwarf scrub (51), shrub/scrub (52), and grassland/herbaceous (71) vegetation. We focused on the

amount of natural land cover within 2 km as a landscape-scale factor because it is an indicator of landscape complexity and local on-farm biodiversity in most pest control and agroecology studies (Tschamtkke et al. 2007, Martin et al. 2016, Karp et al. 2018). Using spatial statistics tools in ArcGIS (v 10.1; ESRI 2011), zonal histograms identified the total proportion cover of the NLCD natural land cover classes present within each buffer. Here, a high total proportion of natural land cover in the landscape indicates high landscape complexity, and a low proportion indicates low landscape complexity.

**Analysis**

To test how differences in local vegetation, temperature, and landscape factors predict plant damage (Table 2), we built mixed effects models for each focal crop (*Brassica*, cucurbit, tomato) informed by our hypothesized relationships (Fig. 1). We analyzed ten types of plant damage across the three crops: four variables for *Brassica* at the plant scale, two variables for cucurbits at the plant and garden scale, and three variables for tomatoes at the plant and garden scale.

Mining damage on *Brassica*, fruit damage on cucurbits, and sun and disease tomato fruit damage were negligible (Table 2), so we did not analyze these data. The dependent variables for each crop plant included all of the local and landscape factors as covariates and an interaction term between the number of herbaceous plant species and natural land cover in the landscape to test for a significant local–landscape interaction. We included sampling date and garden site as random effects in all models.

For *Brassica*, we created four response variables to analyze (1) amount of leaf damage from insect chewing damage (mean leaf area with chewing damage), (2) amount of leaf damage from insect sucking damage, (3) amount of leaf damage from disease damage, and (4) amount of total leaf damage. To test how local and landscape factors predict *Brassica* damage, we modeled the average amount of leaf area damaged from chewing, sucking (log-transformed), and disease (log-transformed) per site per sampling period as the response variable using a Gaussian distribution in generalized linear mixed models (GLMMs) and linear mixed models (LMM). The models included *Brassica* conspecific density within the garden as a covariate and average plant volume (height  $\times$  width) as offset term to account for sampling area. An offset term is a known component of the linear predictor variable that requires no coefficient (McCullagh and Nelder 1989).

For cucurbits, we created two response variables to test how local and landscape factors predict cucurbit damage at the plant scale and garden scale: (1) log-transformed pooled average number of leaves with powdery mildew damage per site per sampling period (plant scale) and (2) the number of plants with powdery mildew and plants without powdery mildew within the garden (garden scale). For the plant scale model, we fit the full model with a Gaussian distribution in a LMM. For the garden scale model, we used the `cbind` function to create a matrix of the number of plants with powdery mildew and without powdery mildew as the response and fit the model with a Binomial distribution in a GLMM. To test whether natural enemy presence predicts plant damage, we similarly modeled the number of leaves with powdery mildew with the presence of *Psyllobora* as the covariate in a LMM.

For tomatoes, we created three response variables to test how local and landscape factors predict tomato damage at the plant scale and garden scale: (1) pooled average of fruits with herbivory damage (plant scale); (2) pooled average values of all fruit damage (herbivory, disease, sun) across the site (plant scale); and (3) the number of plants with and without wilt within the garden (garden scale). For plot scale fruit damage, we log-transformed plant scale values and we removed three sites where there were no consistent numbers of tomato individuals to sample to maintain our random effects. For the garden scale model, we used the `cbind` function to create a matrix of the number of plants with wilt and plants without wilt as the response and fit the model with a Binomial distribution in a GLMM.

For each full model for each crop plant, we performed model selection using the `dredge` function in the R package `MuMIn` (Barton 2009). The method fits all possible combinations of models of the covariates and compares their ability to best explain or predict the response variable—in this case the amount of leaf or fruit damage for each crop type—using the Akaike information criterion (AICc). The explanatory variables (local vegetation, temperature, landscape factors) were scaled in the models, and VIF scores for all models were  $<3$ . Significance of the explanatory variables is taken at  $p \leq 0.05$ . Model fit for each model was estimated using AICc relative to a null model (Burnham and Anderson 2002). Analyses were performed in the R statistical environment (R Development Core Team 2016).

## RESULTS

Plant damage on *Brassica*, cucurbits, and tomatoes varies in form and in magnitude across the gardens (Tables 2, 3). The percent of leaf area damaged on *Brassica* highly varied across all sampled plants and by damage type (Table 2). The most prevalent disease damage on *Brassica* included white spot, bacterial leaf spot, and white rust (Table 3). Powdery mildew damage on cucurbit leaves was prevalent, but fruit damage was minimal. Of 180 sampled cucurbit plants across the season, 58.9% had powdery mildew damage on their leaves. Few plants had sun, herbivore, or mildew damage; in only one case, a



plant had both fruit herbivory and sun damage. Fruit damage on sampled tomato plants included herbivory, disease, and sun scorch. The most prevalent diseases on tomato included late blight, black mold, and bacterial leaf spot (Table 3). The proportion of tomatoes with disease ranged from 0% to 87% of plants, with an average of about a quarter of plants. Disease damage was seasonal and only observed in the late summer season (August). The prevalence of powdery mildew on cucurbits and tomato disease (wilt) in the gardens highly varied across sites. The proportion of cucurbits with powdery mildew at the garden scale ranged from 0% to 100% of plants at a site, but on average about a third of plants had mildew. While we present results from total plant damage as this may be important to production-focused practitioners, we focus on the specific types of plant damage in our results and discussion.

**Local and landscape predictors of plant damage**

The differences in local vegetation, temperature, and landscape factors variably predicted plant damage measures among the three focal crops (Table 4; Fig. 2).

For *Brassica*, the best model predicting the amount of chewing leaf damage included the number of herbaceous plant species in the garden, while the best model predicting the amount of diseased leaf damage included temperature variability, the amount of natural cover, and garden size. Leaf area of disease damage was significantly lower in gardens with more variable temperatures, in smaller gardens, and in gardens surrounded by more natural cover within 2 km. No factors predicted sucking damage and total leaf damage well, and the best model was the null model.

For cucurbits, the best model predicting the number of leaves with powdery mildew at the plant scale included floral abundance,

Table 3. Disease damage observed on focal plant species (*Brassica*, cucurbit, tomato) within the 24 gardens across the sampling period.

Crop	Causal Agent	Scientific Name	Common Name	N	%
<i>Brassica</i>	Bacteria	<i>Pseudomonas syringae</i>	Bacterial leaf spot	51	18.41
	Bacteria	<i>Xanthomonas campestris</i>	Black rot	27	9.75
	Bacteria/ Fungi	<i>Alternaria; Alternaria brassicae</i>	Leaf spot	10	3.61
	Fungi	<i>Pseudocercospora capsellae</i>	White spot	81	29.24
	Fungi	<i>Fusarium oxysporum</i>	Fusarium yellows	24	8.66
	Fungi	<i>Peronospora parasitica</i>	Downy mildew	22	7.94
	Fungi	<i>Erysiphe cruciferarum</i>	Powdery mildew	7	2.53
	Fungi	<i>Mycosphaerella brassicicola</i>	Ring spot	7	2.53
	Fungi	<i>Phytophthora megasperma</i>	Root rot; Phytophthora root rot	2	0.72
	Fungi	<i>Sclerotinia</i>	White rot	1	0.36
	Fungi	<i>Capnodium spp., Fumago spp., others</i>	Sooty mold	1	0.36
	Oomycete	<i>Albugo candida</i>	White rust	43	15.52
	Cucurbit	Fungi	<i>Podosphaera xanthii; Erysiphe cichoracearum</i>	Powdery mildew	106; 934*
Tomato	Bacteria	<i>Xanthomonas campestris pv. Vesicatoria</i>	Bacterial leaf spot	2	16.67
	Fungi	<i>Phytophthora infestans</i>	Late blight	4	33.33
	Fungi	<i>Alternaria alternata</i>	Black mold	3	25.00
	Viral	<i>Phytophthora</i>	Black rot	1	8.33
	Fungi	<i>Alternaria solani</i>	Early blight	1	8.33
	Fungi	<i>Tospovirus</i>	Spotted wilt virus	1	8.33
	Fungi	<i>Fusarium oxysporum f. sp. lycopersici; Verticillium dahliae</i>	Fusarium wilt; Verticillium wilt	1047†	12.78

Notes: Data are the total number of individuals observed on all sampled plants (N) and the percentage of that cause of disease damage on the plants by focal crop (%). Note that tomato and cucurbit include garden scale measurements.

\* Count of total number of cucurbit plants at the garden scale across all sampling periods.

† Count of total number of plants with disease at the garden scale across all sampling periods.

Table 4. Results of the mixed models built with local and landscape factors that best predicted plant damage measures for the three focal crop plant species determined using model selection.

Crop and scale	Response	Predictor	Coefficient	SE <sub>Adj</sub>	z	P	AIC <sub>c</sub>
Brassica Plant	Chewing damage	Intercept	2.92	0.27	10.74	<0.001	223.36
		Herb. Plant Spp	-0.40	0.22	1.77	0.08	
	Sucking damage (log)†	Intercept	1.22	0.25	4.80	<0.001	132.80
		No. Trees and shrubs	0.12	0.10	1.20	0.23	
	Disease damage (log)	Intercept	0.04	0.22	0.16	0.87	190.22
		Temp SD	0.52	0.23	2.26	0.02	
		% Natural cover (2 km)	-0.60	0.26	2.28	0.02	
	Total leaf damage (log)†	Garden size	-0.46	0.22	2.04	0.04	
		Intercept	2.00	0.11	17.80	<0.001	109.74
		% Woodchip mulch	-0.09	0.07	1.23	0.22	
Cucurbit Plant	Leaf powdery mildew (log)	Intercept	2.13	0.32	6.71	<0.001	160.43
		No. Flowers	-0.25	0.10	2.36	0.02	
		Herb Plant Spp	0.42	0.11	3.76	<0.001	
	Leaf powdery mildew (log)	% Natural cover (2 km)	-0.39	0.12	3.43	<0.001	
		Intercept	2.03	49.00	12.02	<0.001	160.43
Garden	Damaged : Healthy plants	No. <i>Psyllobora</i>	0.42	49.00	2.36	0.02	
		Intercept	-0.87	0.66	1.31	0.19	369.80
		Temp SD	0.33	0.13	2.60	0.01	
		No. Flowers	-0.35	0.08	4.54	<0.001	
		Herb Plant Spp	0.21	0.08	2.65	0.01	
		% Natural cover (2 km)	-0.63	0.13	4.69	<0.001	
		Garden size	-0.48	0.14	3.48	<0.001	
Tomato Plant	Fruit herbivory damage (log)	No. Trees and shrubs	0.07	0.12	0.62	0.53	
		Intercept	-1.73	0.01	140.58	<0.001	63.67
		No. Trees and shrubs	-0.72	0.01	69.17	<0.001	
	Fruit damage	Temp SD	0.15	0.01	23.84	<0.001	
		Intercept	-1.09	0.54	2.01	0.04	85.63
Garden	Damaged : Healthy plants	No. Trees and shrubs	-0.40	0.23	1.73	0.08	
		Intercept	-1.73	0.54	3.24	0.001	412.03
		Herb Plant Spp	0.23	0.08	2.67	0.008	
		% Natural cover (2 km)	0.11	0.23	0.49	0.63	
		Local × Landscape	0.34	0.08	4.50	<0.001	
		% Woodchip mulch	-0.12	0.14	0.84	0.40	

Notes: See text and Table 2 for details on variables used in the analysis. Local × Landscape indicates interaction term between the number of herbaceous plant species and the amount of natural habitat land cover in the landscape within 2 km surrounding a garden. Colon (:) indicates the proportion of damaged to healthy plants. Coeff., coefficient; SE<sub>Adj</sub>, standard error (adjusted); SD, standard deviation; z, z-value; P, P-value at 95% confidence; and AIC<sub>c</sub>, Akaike's information criterion for small sample size.

† Best fit model with lowest AIC<sub>c</sub> was the null model; we present next best fit model.

herbaceous plant species richness, and the amount of natural cover. Leaf powdery mildew on plants was significantly lower in gardens with more flowers and surrounded by more natural cover, but significantly higher in gardens with more herbaceous plant species. In addition, the presence of *Psyllobora* lady beetles on cucurbit plants was significantly positively correlated with the average number of leaves with powdery mildew. At the garden scale, the proportion of cucurbit plants with powdery mildew was best predicted by temperature variability, floral

abundance, herbaceous plant species, the number of trees and shrubs, garden size, and the amount of natural land cover in the landscape. The proportion of cucurbit plants with mildew was significantly higher in gardens with more variable temperatures and more herbaceous plant species, whereas it was significantly lower in gardens with more flowers, in larger gardens, and in gardens surrounded by more natural land cover.

For tomatoes, the best model predicting tomato herbivory fruit damage included the

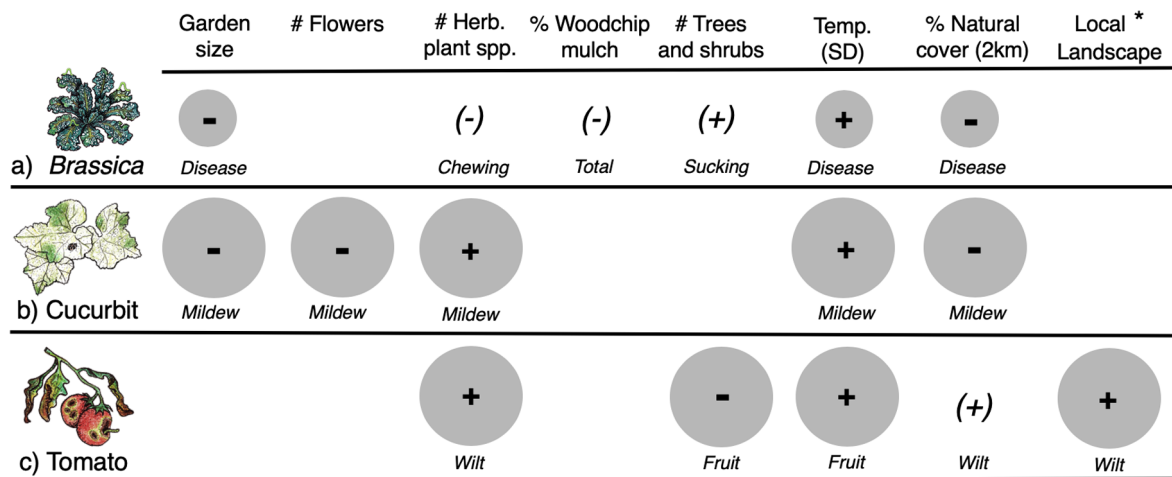


Fig. 2. Simplified visual summary of the relationships between plant damage measures and local vegetation, temperature, and landscape factors (top x-axis) at either the plant or garden scale for each of the focal crop species (y-axis) of *Brassica* (a), cucurbits (b), and tomato (c). Important factors from the best models are represented by gray circles, where size of the gray circle represents the degree of significance (larger circles  $P < 0.01$ ; smaller circles  $0.01 < P < 0.05$ ). Directionality of significant factors shown within circles as either positive (+) or negative (-), with insignificant factors in models represented as directionality within parentheses ((+)) and no circle. Text below circles indicates disease type (“chewing,” “mildew,” etc.). Models shown are at the plant scale (a), at the garden scale (b), or at both scales (c). See Table 4 for model results for further interpretation.

number of trees and shrubs and temperature variability. Tomato herbivory fruit damage was significantly higher in gardens with fewer trees and shrubs, and with more variable temperatures. The best model predicting all fruit damage included the number of trees and shrubs. At the garden scale, the proportion of tomatoes with tomato wilt disease was best predicted by the number of herbaceous plant species, mulch woodchip ground cover, the amount of natural land cover in the landscape, and the interaction between herbaceous plant species and natural land cover. The proportion of tomato plants with wilt disease was significantly higher in gardens with more herbaceous plant species and surrounded by more natural land cover, with the positive effect of herbaceous plant species increasing with increasing with greater amounts of natural land cover in the landscape.

**DISCUSSION**

We investigated local and landscape factors associated with plant damage on three common crop species in urban agroecosystems using

urban community gardens as a model system. We found that local and landscape factors significantly predict herbivore and disease damage, but that the importance of these factors and the direction of the association vary with crop species and damage type. We discuss the biotic and abiotic local and landscape factors associated with plant damage and the urban agroecological applications.

**Local and landscape factors predict plant damage**

In support of our hypotheses, higher amounts of local vegetation complexity (e.g., trees and shrubs) and landscape complexity (percent natural land cover) are associated with lower incidence of some measures of herbivore and disease damage in gardens. Specifically, we found that tomato fruit damage from herbivores and disease was lower in gardens with more trees and shrubs, powdery mildew prevalence is lower in gardens with more flowers, and amounts of chewing damage on *Brassica* leaves are lower in gardens with more herbaceous plant species. Arboreal vegetation through agroforestry may enhance agroecosystem structural complexity,

provide alternative food resources to divert potential crop herbivores, and moderate microclimate to reduce disease prevalence both above and below ground (Pumarino et al. 2015). More plant diversity through flowering plants may provide food resources for natural enemies that protect plants from insect and pathogen pests. Although we did not measure top-down pest regulation, these findings seem to support agroecological theories and conservation biological control practices positing that greater habitat heterogeneity through structural and functional diversification can promote pest control by lowering resource concentration for herbivores and boosting natural enemies (Altieri et al. 1983, Altieri 2002).

Yet, we found mixed effects of herbaceous plant species richness in regard to crop disease damage, supporting the argument that increasing plant diversity to mitigate pest impacts is not a straightforward management guideline in urban environments (Dale and Frank 2018). Both powdery mildew and tomato wilt at the garden scale were more prevalent in gardens with more herbaceous plant species. The epidemiology of crop disease predicts that crop mixtures should dampen disease epidemics by reducing disease spread likelihood between conspecific plants. However, the presence of one highly susceptible reservoir species could increase pathogen prevalence of other species through pathogen spillover (Power and Mitchell 2004). Thus, disease outbreaks may increase within agroecosystems if plant species are introduced that harbor or are vulnerable to certain diseases shared by other crop species within the system. The spatial distributions and phylogenetic relatedness of different plant species may also be important for managing disease outbreaks (Schroth et al. 2000). In our case, even a few garden plots with only cucurbits or only tomatoes could act as pathogen sources to surrounding plots, even if those plots are themselves specious. Habitat size could mitigate these effects through dilution and pathogen dispersal limitation, and this could explain why garden size reduces powdery mildew prevalence at the garden scale. Within a crop type, varietal differences in terms of resistance to insects and pathogens may also be important for influencing plant resistance to insects and pathogens (Wolfe 1985, Zhu et al. 2000). Community gardens are

thus complex from an epidemiological perspective because they harbor many plant species (e.g., food crops, exotic ornamentals, and native vegetation) and varieties (e.g., heirloom tomatoes, cultivars of burpless cucumbers, kale varieties) and interspecific plant interactions. Furthermore, pest spread within the garden depends on the management decisions and practices used by many people. Future studies should investigate how varietal differences, spatial distribution, and different management strategies influence plant damage within urban production systems.

We found that plant damage in urban agroecosystems is also associated with landscape context and that effects of local factors can depend on landscape context. In accordance with our hypothesis, gardens surrounded by more natural land cover had lower cucurbit powdery mildew prevalence and less *Brassica* disease leaf damage. In urban landscapes, plant pathogen outbreaks can heighten with increased urbanization due to loss of native forest cover and introduced ornamental plant species harboring pathogens (Paap et al. 2017, Roman et al. 2018), or novel insect pests associated with fungal pathogens that burgeon in urban areas (Ploetz et al. 2013, O'Donnell et al. 2016). The results here on disease damage suggest that natural habitat within the landscape is (1) reducing pathogen dispersal and there are fewer source habitats for crop diseases in these landscapes or (2) supporting natural enemies that provide top-down disease control (Plantegenest et al. 2007). We found an important interaction between local and landscape factors on tomato wilt prevalence in gardens, where the positive effect of herbaceous plant species on wilt prevalence increased in gardens surrounded by more natural land cover. The positive interaction on tomato disease prevalence is interesting because tomato fungal and viral diseases (e.g., fusarium wilt and verticillium wilt) are often soil-borne and moisture-dependent (see below). Many of the gardens in more complex landscapes surrounded by more natural land cover receive more coastal fog or are located in agricultural regions, suggesting that other abiotic or cultural factors including fog-facilitated dispersal and land use history are important. Though the influence of landscape context on crop disease spread in urban landscapes is largely unknown,



urban agroecosystems may face more challenges managing certain bacterial and fungal diseases with increasing urbanization (densification and expansion) and the loss of (semi-)natural habitats.

We found some differences in how local and landscape factors are associated with plant damage from herbivores of different feeding guilds. Chewing damage on *Brassica* decreased with increasing herbaceous plant species, while sucking damage generally was higher with higher abundance of trees and shrubs. In urban green-spaces, the response of herbivores to vegetation management can be species-specific or feeding-guild-specific (Raupp et al. 2010). For example, on golf courses, residential gardens, and parks, herbivores positively associate with vegetation volume, but the association with vegetation diversity within the habitat depends on the particular herbivore species and presumably their functional traits along with plant species identity (Mata et al. 2017). It is surprising that we found no association between the landscape and *Brassica* herbivore damage, because our previous work has linked lower pest regulation of herbivores in gardens surrounded by more urban and agricultural land cover (and less natural land cover) in the landscape (Philpott and Bichier 2017). Furthermore, scale insects, aphids, mites, and leaf miners often increase in urban areas due to dispersal limitation and higher fecundity, and the loss of their natural enemies that provide top-down control (Shrewsbury and Raupp 2006, Raupp et al. 2010). Other studies have also shown increased mining damage (Kozlov et al. 2017) and increased chewing damage (Cuevas-Reyes et al. 2013) in more urban areas, though opposite trends have also been found (Moreira et al. 2019). In sum, our results further exemplify the complex, often non-linear relationships between ecological factors, herbivores, and herbivory in urban environments (Raupp et al. 2010, Dale and Frank 2018).

#### *Temperature variability and plant damage*

In our study, greater temperature variability within urban agroecosystems associated with higher plant damage, particularly by plant diseases, demonstrating that changes in local microclimate are also important for disease dynamics. More variable temperatures were overall

associated with higher amounts of plant damage from disease and mildew across crop species. Here, urban agroecosystems that experience higher temperatures or greater interday variation in temperatures are exposed to more extreme heat. Powdery mildew and tomato wilt prevalence at the garden scale and the amount of *Brassica* disease damage on plants were higher in gardens with more variable temperatures. The biology of crop plant diseases could explain these different responses. For example, fungal disease spread via spore dispersal is dependent on temperature and moisture in the environment (Colhoun 1973). Powdery mildew thrives in warmer and drier conditions rather than moist and cool conditions, whereas several *Brassica* diseases disperse through air moisture and depend on soil temperature and moisture (Koike and Subbarao 2003). Gardens that are in denser, built-up areas with more urban cover may be less susceptible to some crop diseases if those gardens are less likely to experience pathogen colonization through wind and moisture. Interestingly, tomato herbivore fruit damage by small mammals and birds was also higher in gardens with more variable temperatures. This suggests that more variable conditions of greater temperature extremes may either increase foraging activity of herbivores or alter herbivore foraging strategy if more variable weather patterns cause risk-sensitive foraging behavior (Caraco et al. 1990, Monaco and Hel-muth 2011). The results here support urban agriculture findings in southern cities where crop exposure to high temperature extremes can increase susceptibility to herbivores and disease (Eriksen-Hamel and Danso 2010). In the urban forest, tree species are still susceptible to pests under extreme heat despite intensive management (Kendal et al. 2018). This is because even short-term exposure to extremes can have large and long-term impacts on crops through effects on herbivore and disease pest ecology (Coakley 1988, Rosenzweig et al. 2001, Bale et al. 2002). Thus, even if urban farmers and gardeners readily respond to changing weather patterns to maintain their plants, temperature still plays an important role in disease dynamics, crop survival, and food production. Temperature impacts on crops have implications for urban agriculture in relation to climate change, particularly in cities in California where temperatures and weather



events (heat, drought) are becoming more extreme.

#### *Natural enemies and plant damage*

We documented a strong positive association of *Psyllobora*—a mycophagous (fungus-feeding) lady beetle—with the presence of powdery mildew on cucurbits. Natural enemies and antagonists in agroecosystems are population regulation mechanisms that provide system-level resilience to pests and disease (Bianchi et al. 2006, Vandermeer et al. 2010). The positive association between *Psyllobora* and powdery mildew shows a density-dependent response of natural enemies to pest outbreaks, similarly demonstrated in greenhouse studies (Sutherland and Parrella 2009). Powdery mildews are an important plant pathogen in agriculture that cause significant yield losses in cucurbits (Miller et al. 2003), and many gardeners in our system use homemade bicarbonate solution with baking soda to prevent mildew establishment on cucurbits. We cannot determine from our study if higher *Psyllobora* densities translate to effective control of powdery mildew because we did not measure disease removal. Nor can we provide support for the enemies hypothesis because, while greater plant cover and species richness can promote natural enemies, powdery mildew positively associated with herbaceous plant species richness. Thus, the mechanisms underlying powdery mildew control in this system are unclear.

Although we did not specifically test this, the effects of local and landscape factors on herbivore damage could be a result of top-down indirect effects. Many of the diverse array of natural enemies in these agroecosystems, including those from Araneae, Aves, Carabidae, Coccinellidae, and Hymenoptera, are affected by local factors, such as vegetation diversity and composition, and by landscape factors, such as landscape composition (Otoshi et al. 2015, Burks and Philpott 2017, Egerer et al. 2017b, 2018, Philpott et al. 2019). In addition, experimental work in these systems indicates that pest removal is also affected by garden ground cover, vegetation (complexity, diversity), and landscape context (Philpott and Bichier 2017). Thus, in this study, the low leaf damage of *Brassica* plants in gardens with more woodchip mulch and more herbaceous plant species could be explained by the

effects that these factors have on natural enemies that then cascade down to herbivores and, ultimately, to plant damage. In fact, the amount of woodchip mulch and herbaceous plant species positively correlates with higher activity of ground-dwelling spiders and carabid beetles in these agroecosystems (Otoshi et al. 2015, Philpott et al. 2019). It is interesting that we found lower fruit damage in gardens with more arboreal vegetation because agroforests may support mammal and bird pests (Pumarino et al. 2015). Soil management practices and water use by gardeners may also affect pest outbreaks and pest regulation in gardens through effects on plant condition (e.g., plant size, nutrient content, water stress; Archer et al. 1995), to increase likelihood of plant damage (Kim and Underwood 2015). In our system, soil-related factors only indirectly affect herbivore pest regulation through direct effects on plant volume (Egerer et al. 2018). Because we accounted for plant size in our analysis, we cannot make strong linkages between soil and water management and crop damage here. In sum, though agroecosystems are in constant ecological flux and our sampling for one natural enemy species (and plant damage in one season) captures a static measure of a dynamic process in relation to certain local and landscape factors, this work informs the ecology of plant damage and protection in urban contexts.

#### *Agroecological applications*

Urban farmers and gardeners face unique challenges in their efforts to produce food crops utilizing agroecological methods in urban environments (Altieri et al. 1999, Eriksen-Hamel and Danso 2010, Tiffany 2017). Many also report lack of urban agroecological resources and training, for example, from Cooperative Extension Services in the USA (Oberholtzer et al. 2014, Surls et al. 2014). This study fills knowledge gaps because most of these urban farmers (92.4%;  $N = 189$ ; unpublished data, the authors) report pest-related challenges and use hand removal, homemade sprays and tonics to combat damage by arthropods, snails, and small mammals (the authors, unpublished data). Even relatively small amounts of herbivory such as those documented in this study (~10%) can determine differences in plant fitness and reproduction (Crawley 1985). Perhaps more importantly for the urban farmer

and gardener, plant damage may reduce the amount of marketable or usable food given consumer preferences for damage-free produce (Thompson and Kidwell 1998, Yue et al. 2007, Oberholtzer et al. 2014). Though we did not measure yield here, we suggest that the findings from this work can be applied by people to grow food in cities using agroecologically based conservation biological control practices and to boost yield production through agroecosystem vegetation management. Given capacity and ability, urban farmers and gardeners can incorporate trees and shrubs (Smith et al. 2006, González-García et al. 2009), provision floral resources (Landis et al. 2000, Shrewsbury et al. 2004, Rebek et al. 2006, Bennett and Gratton 2012), and create heterogenous ground cover habitat (Tamburini et al. 2016) for beneficial natural enemies to reduce insect and disease plant damage. Many of these recommendations in both rural agricultural and urban ecosystems echo sustainable agroecological practices including conservation biological control for urban agroecosystems aimed at enhancing local habitats for beneficial insects and species interactions to promote pest control (Altieri and Nicholls 2018, Arnold et al. 2019).

Urban farmers must also acknowledge and manage for the multitude of trade-offs in their management decisions. In these heterogenous systems, effects of abiotic and biotic local and landscape factors on crop plant damage depend on crop species and damage type, and different factors associate with herbivore- versus disease-mediated damage. Practitioners can add woodchip ground cover to possibly increase habitat for spider natural enemies that protect *Brassica*, but this habitat feature may detrimentally affect ground-nesting pollinators essential to pollination (Quistberg et al. 2016). Crops may suffer less insect or disease damage in gardens with more trees and shrubs (e.g., tomatoes in this study), but yields could suffer as plant growth and fruit production are greatly affected by shading (Cockshull et al. 1992). More stable temperatures in urban agroecosystems may allow for more species to grow due to less exposure to extremes (Egerer et al. 2019), but more plant species richness may lead to pathogen spillover from susceptible disease hosts. Thus, various designs of local agroecosystems lead to different ecological

interactions (either positive or negative) at multiple scales, with different effects on crop production and ecosystem service synergies (Smukler et al. 2012). This work highlights some of these management complexities by studying three physiologically different crops. Utilizing basic agroecological practices in combination with local knowledge of the environment should aim to optimize damage reduction, increase acceptable production levels, and overall improve sustainable urban food production.

## CONCLUSION

Ecological theories in agroecology predict that system-level resilience to insect and disease pests occurs through mechanisms including greater habitat structural and functional diversity, and the maintenance of natural enemies. Agroecosystems that incorporate more structural complexity and diversity through diverse plant assemblages, and functional diversity through greater floral and arboreal vegetation should better maintain an ecological equilibrium necessary for urban food production. Our work shows that urban agroecosystems are vulnerable to insect and disease pests, but that some local agroecological diversification strategies are associated with lower plant damage. Increasing floral abundance, incorporating agroforestry, and increasing ground cover heterogeneity are some of these practices. Yet, urban agroecosystems are embedded within the social–environmental context of their broader environment. A combination of factors largely outside of practitioners control including agroecosystem size, natural habitat cover in the surrounding landscape, and temperature fluctuations all matters for plant susceptibility to insect and disease pests. Thus, urban densification and climate change will increasingly challenge urban agroecosystem sustainability and should be considered by urban planning and policies for urban agriculture. Nevertheless, it remains crucial to increase habitat heterogeneity and maintain speciose natural enemy communities in urban agroecosystems to support intrinsic plant protection. The ability of local management to combat plant damage through agroecological approaches will be essential to ensure the sustainability and production capacity of agriculture in cities.

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