



The relationship between pollinator community and pollination services is mediated by floral abundance in urban landscapes

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Abstract

It is often argued that biodiversity and ecosystem functioning are linked by both habitat and species composition, and that this relationship is particularly critical for mobile ecosystem service providers. This may be especially true for pollinators, which are essential for the reproduction of the majority of flowering plant species, are highly mobile, and can exhibit dramatically different foraging behaviors across ecosystems. Understanding how habitat and community composition impact pollination is especially relevant in urban environments where pollinators can promote food security. We examined the relationships between local resource density, landscape composition, pollinator abundance and richness, and pollination services in an urban agricultural system spanning >125 km of the California central coast. We used a replicated, experimental approach to evaluate the reproductive success of jalapeño peppers across urban gardens and conducted a greenhouse experiment to evaluate the benefits of insect-mediated pollination to pepper reproduction. In the greenhouse, we found that jalapeño fruit weight and seed number was significantly greater with insect-mediated pollination than without. In the field, we found that jalapeño seed number increased significantly with herbaceous (weed, crop, and ornamental) plant richness and the number of perennial trees and shrubs at the site level, but decreased with the amount of natural landscape cover. We also found that higher pollinator richness enhanced seed number in floral-dense gardens, likely due to the greater functional complementarity of a more diverse pollinator community. Furthermore, there was a positive relationship between pollinator abundance and seed number, but it weakened in gardens with more flowers, likely through lower per-plant pollinator visitation in the presence of competing floral resources. As in past studies, we found that mulch had a negative impact on pollinator abundance, highlighting that abiotic factors commonly managed by gardeners can directly impact ecosystem service providers. This study demonstrates that local conditions can significantly influence ecosystem service provision and that urban gardeners need to optimize for both pollinator richness and floral resource availability to achieve optimal pollination.

Keywords Pollination · Urban agriculture · Biodiversity · Ecosystem function

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Introduction

Biodiversity is rapidly declining as a result of numerous global change drivers (Butchart et al. 2010; Tittensor et al. 2014), threatening ecosystem functioning and services that are essential for human well-being (Loreau et al. 2001; Hooper et al. 2005; Balvanera et al. 2006; Naeem et al. 2009; Cardinale et al. 2012). This relationship (biodiversity-ecosystem-function, or BEF) has been the focus of many studies within rural agricultural systems that strive to understand food security, pest suppression, and other ecosystem services. Though these studies have largely found strong, positive relationships between biodiversity and ecosystem functioning (Larsen et al. 2005, Tschamtkke et al. 2005, Tschamtkke et al. 2012, but see Cardinale et al. 2006), the mechanisms underlying this relationship are less understood. Further, while ecosystem

functioning is often mediated by biotic and abiotic factors at multiple spatial scales (Maire et al. 2012), and by the foraging patterns of mobile ecosystem service providers (Kremen et al. 2007; Hoehn et al. 2008; Albrecht et al. 2016), the relative role of local resource levels in shaping animal foraging and resulting ecosystem services is not typically evaluated. Specifically, the diversity and abundance of food resources may serve to either potentially concentrate (Williams et al. 2015; Xie et al. 2019) or dilute (Veddeler et al. 2006) foraging organisms at resource patches, but this phenomenon is rarely quantified outside of rural agricultural systems (but see Jha and Vandermeer 2009).

The relationship between local resources, landscape composition, and biodiversity may be particularly important for pollinators, whose movement patterns directly impact ecosystem service provisioning (Kremen et al. 2007). This is because pollinators, which are essential for the reproduction of more than 80% of flowering plant species (Ollerton et al. 2011), are both highly mobile and exhibit tremendous variation in community characteristics such as plant visitation behaviors (Burkle and Alarcon 2011). While pollination service indices, such as plant reproduction, are often a function of the richness and abundance of the wild pollinator community (e.g. Gómez et al. 2007; Lowenstein et al. 2015), the ability to deliver pollination services may also be contingent on local and landscape habitat factors. In rural agricultural systems, pollinator abundance and richness (e.g. Kennedy et al. 2013; Goulson et al. 2015), as well as pollination services (e.g. Potts et al. 2010; Cusser et al. 2016), are often mediated by landscape drivers such as agricultural intensification and natural habitat cover (e.g. Kim et al. 2006; Kennedy et al. 2013; Blaauw and Isaacs 2014a).

In addition to landscape factors, local floral diversity, abundance, and composition can mediate pollination through impacts on pollinator densities (Steffan-Dewenter and Westphal 2008; Williams et al. 2015), foraging dynamics (Kunin and Iwasa 1996; Kunin 1993), visitation rates (Van Nuland et al. 2013; Veddeler et al. 2006), and pollen deposition (Lortie and Aarssen 1999; Evans et al. 2017). Classic research in foraging biology has shown that, when a limited number of foragers spread out in a high resource patch, it can reduce per-plant visitation, something called the “dilution effect” (Root and Kareiva 1984; Yamamura 1999). In contrast, when high resource patches recruit more foragers to a site, increasing per-plant visitation, it is known as a “concentration effect” (Sih and Baltus 1987; Kunin 1993; Totland and Matthews 1998). Dilution and concentration effects, respectively, reduce or enhance forager visitation rates, with implications for plant reproduction. Dilution may also occur when, at high floral densities, co-flowering heterospecific plants result in interspecific competition for pollinators, reducing plant visitation (Ghazoul 2006). Furthermore, floral fidelity may be relaxed in communities with high plant diversity, increasing inter-

specific pollen transfer (Fontaine et al. 2008) and inhibiting pollination (Wilcock and Neiland 2002; Holland and Chamberlain 2007).

In agricultural systems, both foraging dilution and concentration responses to floral resources are sensitive to scale (Veddeler et al. 2006, Jha and Vandermeer 2009, Riedinger et al. 2013, Holzshuh et al. 2016) and pollinator species composition (Jha and Vandermeer 2009), likely because pollinators vary in foraging behavior and foraging distance (Greenleaf et al. 2007; Pisanty et al. 2015). Indeed, beyond pollinators, there is a strong link between species trait diversity and ecosystem function that has been documented across taxa and ecological systems (Naeem and Wright 2003; Cardinale et al. 2004; Cardinale et al. 2006; Hooper et al. 2005; Schleuning et al. 2014). For pollinators, communities exhibiting a diversity of functional traits provide greater pollination resources (Hoehn et al. 2008; Cadotte et al. 2011; Gagic et al. 2015), but the relationship between pollinator diversity and pollination may be dependent on local floral conditions (Tylianakis et al. 2008). In this study, we experimentally evaluate how pollination services are mediated by both landscape context and the interactions between local floral resources and pollinator abundance and richness in an understudied system, urban agriculture.

Urban systems are compelling habitats in which to investigate these interactions. Urban gardens are important sites for food production (McCormack et al. 2010) and serve as important refuges for pollinator communities within cities (Fetridge et al. 2008; Matteson et al. 2008; Frankie et al. 2009; Matteson and Langellotto 2010; Pardee and Philpott 2014; Burr et al. 2016; Quistberg et al. 2016). A number of studies have found that local habitat features, like the availability of bare ground, can positively impact pollinator abundance and richness in gardens, especially for ground-nesting bees (Quistberg et al. 2016; Ballare et al. 2019). Bare, unpaved ground can also impact crop fruit set (Bennett and Lovell 2019). While some urban studies have found that increased floral abundance at local spatial scales positively impacts pollinator richness (Pardee and Philpott 2014; Quistberg et al. 2016), pollinator abundance (Bennett and Lovell 2019) and pollination (Potter and LeBuhn 2015; Lowenstein et al. 2015), others have found no beneficial impact of increased floral resources (Glaum et al. 2017); this variation may be a result of the dynamic relationship between floral resources and pollinator foraging, in which the composition, diversity, and abundance of floral resources is theorized to either concentrate or dilute pollinators across a landscape (Veddeler et al. 2006). Despite the importance of crop production within urban systems, the impact of the interaction between floral resources and pollinator abundance and richness on pollination services has not been quantitatively evaluated.

In this study, we use a replicated experimental approach to evaluate the reproductive success of jalapeño peppers in

gardens spanning more than 125 km of urban habitat to quantify the links between pollinators and pollination function across heterogeneous landscapes. Urban gardens are important places for the evaluation of pollination services given their ecological, cultural, and economic value to humans (Bellows et al. 2003; Baker 2004; Freeman et al. 2012; Goddard et al. 2013). We used jalapeño peppers as a model system because they are commonly cultivated in urban gardens and may benefit from insect visitation (Delaplane and Mayer 2000), though the benefit of this visitation has not been investigated across heterogeneous field conditions. While past experiments in urban garden studies have focused on bee-pollinators, non-bee pollinators are important contributors to crop production (Rader et al. 2009), so we include both bee and non-bee pollinators in our study. Non-bees include flies (Diptera), which are often generalists that visit multiple plant species (Kearns 2001). Although butterflies (Lepidoptera) and wasps (Hymenoptera) are often considered inefficient pollinators, visitation rates to crop plants by pollinators are often mediated by complex, indirect interactions between species (Primack and Inouye 1993). The pollination success of insect-pollinated plant species is therefore usually not dependent on single, highly specialized pollinator species, but rather on a diverse community of pollinators (Greenleaf and Kremen 2006, Steffan-Dewenter and Westphal 2008, Albrecht et al. 2012 Garibaldi et al. 2016).

In this study, we evaluate three hypotheses: 1) successful reproduction of jalapeño peppers requires insect-mediated pollination, 2) local floral resources and bare ground cover drive pollinator richness and abundance, 3) and jalapeño pollination success is positively related to the interactions between local floral resource availability and pollinator abundance and richness.

Methods

Field study: Characterization of the study sites

The field study was conducted in July 2016 in 21 urban community gardens, 16 of which have been investigated for urban ecological studies for multiple years (e.g. Otoshi et al. 2015; Quistberg et al. 2016; Egerer et al. 2017). The 21 gardens are separated by a minimum of 21 km and range in size from from 444 m² to 15,525 m² (mean 4419.4 ± SD 3884.5 m²) and are distributed across three counties (Monterey, Santa Clara, and Santa Cruz) in the California central coast (Fig. 1). Each garden is a community garden managed in allotments or collectively and each garden contained vegetable and fruit crops and had been actively cultivated between 5 and 49 years. We evaluated both local and landscape characteristics of all the gardens. At the local (within-garden) scale, we measured habitat characteristics within a 20 × 20 m plot placed at the center

of all 21 gardens between July 8th and July 13th of 2016. Specifically, we measured garden size and canopy cover with a convex spherical densiometer at the center of the plot, and 10 m to the N, S, E, and W. We also counted and identified all trees and shrubs as the number of woody plants in the plot. In each plot, we randomly selected eight 1 × 1 m quadrats within which we identified all herbaceous flowering plants (forbs) to morphospecies, measured height of the tallest non-woody vegetation, counted the total number of flowers, and assessed percent ground cover from bare soil, grass, herbaceous plants (crops, weeds, and ornamentals), leaf litter, rocks, and mulch. When counting the number of flowers, we counted flowers inside inflorescences as individual flowers regardless of size.

At the landscape scale, we classified land cover types within 2 km buffers surrounding each garden with data from the 2011 National Land Cover Database (NLCD, 30 m resolution) (Homer et al. 2015). We selected 2 km buffer zones given that bee abundance responds significantly to habitat composition at a 2 km scale (as Kremen et al. 2004). Based on known bee nesting preferences and classification systems used in past studies (e.g., Ritchie et al. 2016; Quistberg et al. 2016; Cohen et al. 2017), we created four land-use categories: 1) natural habitat (including deciduous, evergreen, mixed forests, dwarf scrub, shrub/scrub, and grassland/herbaceous), 2) open habitat (including lawn grass, parks, and golf courses), 3) urban habitat (including low, medium, and high intensity developed land), and 4) agriculture habitat (including pasture/hay and cultivated crop). Other land cover types that covered <5% of the total area were not included. We assessed land cover with ArcGIS v.10.1.

Field study: Pollinator survey

To compare pollinator richness and abundance across 21 sites with different local and landscape features, we conducted visual pollinator surveys in July 2016 along four 4 × 20 m transects that ran E-W in each plot, starting at 0, 5, 10, and 15 m from the southern edge at all sites. Surveys were conducted by one observer and occurred for 30 min between 0:900 and 16:00 on sunny days with less than 50% cloud cover. During each survey we walked the four transects in the 20 × 20 m plot, at a pace of approximately 3.5 min per transect. Because pollination experiments were running at the time of the survey (see below) we did not collect pollinators. Given that active sampling and observational data for pollinator sampling are often highly correlated (e.g. Mandelik et al. 2012), and that observational data is useful for reflecting community-level changes in abundance over space (Kremen et al. 2011), we visually recorded all pollinating insects visiting any flower in the garden, including bees, flies, wasps, and butterflies, and identified each individual to the finest resolution possible (family, tribe, genus, and species). To guide in-field identifications, we brought a box of representative physical

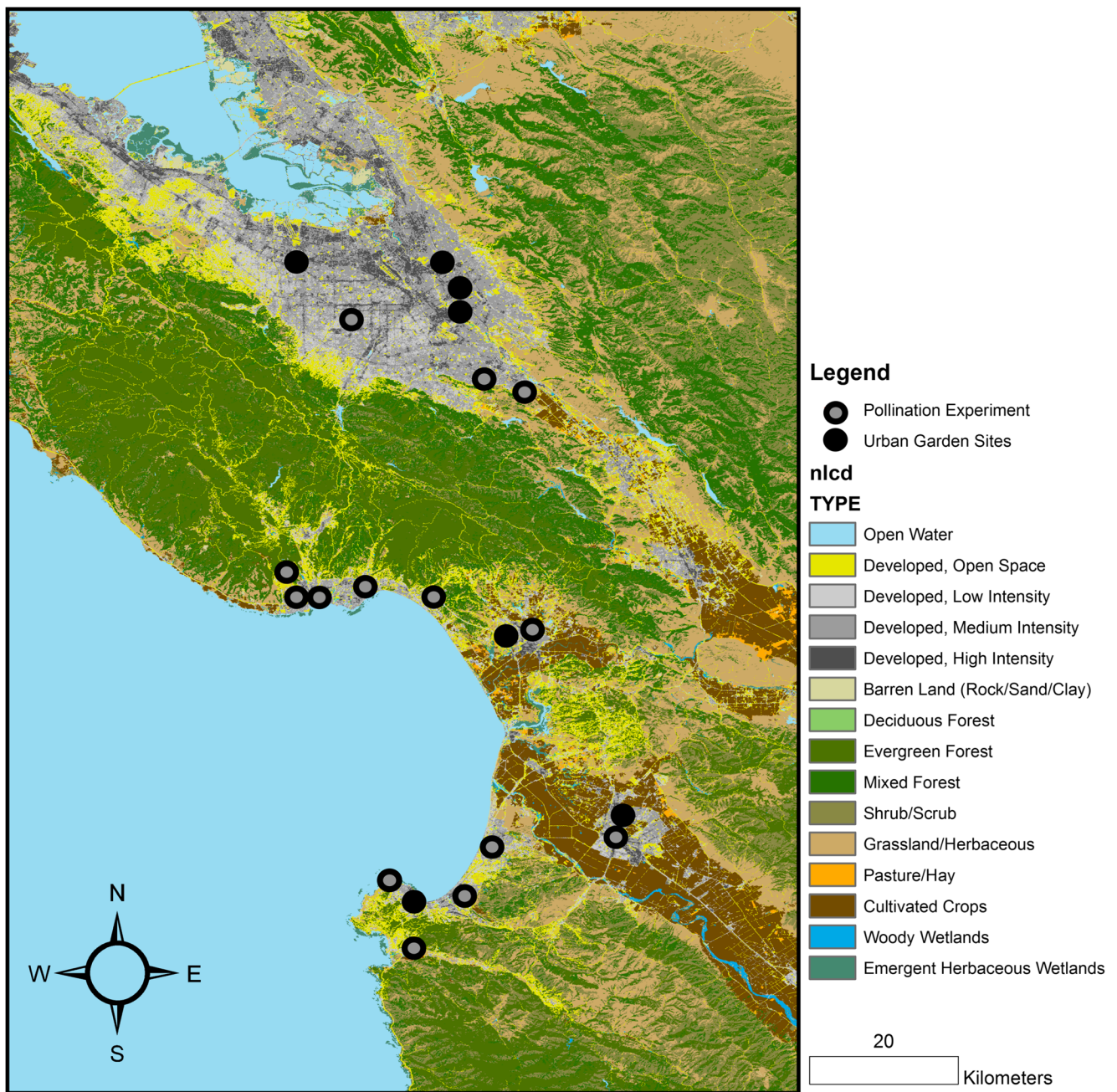


Fig. 1 Map of urban garden field sites along the central coast of California

specimens with us to the field that were previously collected in the same system (see Quistberg et al. 2016); in addition, we consulted online resources (Ascher and Pickering 2017), image databases (e.g. Packer and Ratti 2007), books (Michener 2007), and dichotomous keys (Michener et al. 1994; Gibbs 2010) to create a visual field reference. In-field identifications were conducted by researchers trained in bee identification and systematics according to Michener et al. (1994) at the 2014 Bee Course (American Museum of Natural History). Because visual counts may be subject to observer bias and sampling effort, they were conducted by one individual.

Field study: Pollination experiment

We examined pollination of *C. annuum* jalapeño peppers in a subset of 15 gardens (Fig. 1). We used the ‘Jalapeño’ cultivar of the species *Capsicum annuum* (Solanaceae) as a focal plant because it is an annual crop commonly grown in urban gardens, it has multiple hermaphroditic flowers per plant opening from June–Aug, and because it is attractive to a wide variety of pollinators, including bees (*Dialictus* spp., *Augochlora* spp., *Exomalopsis* spp., *Bombus* spp., *Halictus* spp., *Dialictus* spp., *Hylaeus* spp. (Raw 2000). *C. annuum* cultivars are also

pollinated by flies in the syrphid (Jarland et al. 1997) and tephritid (Vargas and Mitchell 1987) families, as well as by wasps (Bosland and Votava 2000).

We planted *C. annuum* from organic seed in standard soil mixes and grew them in one-gallon pots for 105 days under standard growing and irrigation conditions in a covered outdoor greenhouse at the University of California, Santa Cruz, located within the same geographic region as the study. Upon budding, we placed mesh insect exclusion bags on all peppers until they were utilized for lab or field experiments. Every evening, we tied colored strings on all unopened flowers of all plants in order to record and identify flowers that had opened in the previous 12 h (hereafter ‘recently opened’) at the time of the experiment.

At each garden site we temporarily installed six plants. We placed the six bagged, potted-plants all together as a cluster in random location within the 20 × 20 m plot. We did not place pots in beds, but adjacent to them. The six pepper pots were clustered together in two rows of 3 pots per row, and at a distance of ~20 cm apart from one another. Upon placement in gardens, we randomly assigned three plants into one of three treatments: open (O), open outcross (OO), or a closed (C) treatment to evaluate the importance of outcross pollen to seed and fruit production (Cusser et al. 2016). The remaining plants had bags removed and served as pollen donor plants.

In the open (O) treatment, the bag was opened and one recently opened, virgin flower was randomly selected from the plant and marked, and the entire pepper plant was left unbagged in the field for 48 h to allow visitation by insect pollinators. In the closed (C) treatment, the bag was opened, one recently opened, virgin flower was randomly selected from the plant and marked, and then immediately rebagged for use as a ‘control’ to evaluate the impact of no insect visitation and the experimental manipulation of the bags. The open outcross (OO) treatment received the “maximum” pollination service, a combination of insect visitation and hand-pollination, so that we could evaluate relative pollination limitation in open treatments across the sites (Cusser et al. 2016). In this treatment, the bag was opened, and we randomly selected one recently opened flower and hand-pollinated using flowers from donor plants. Specifically, for the donor plants, we randomly selected four anthers from two randomly selected pollen donor plants (2 anthers per pollen donor). Anthers were removed from the donor using forceps and manually rubbed in a circular motion on the receptive stigma of the closed outcross pollination treatment flower for 2 s each. Plants in this treatment were maintained unbagged in the field for 48 h to allow for insect visitation. After 48 h in the field, plants were picked up, rebagged, and returned to standard sterile indoor greenhouse growing conditions, and then after another 48 h (to ensure that all experimental flowers were completely closed), bags were removed and plants were maintained in greenhouse conditions, free from insect pollinators.

Each plant was allowed to grow for 69 d, when we measured fruit weight (g) and seed number for the fruits in each treatment.

Greenhouse study: Pollination experiment

The greenhouse pollination study was conducted in June–July 2016. Because *C. annuum* may be self-compatible (Pickersgill 1997), we wanted to evaluate the impact of outcross pollination seed pollination (Parker 1997, Benjamin et al. 2014). We therefore evaluated the impact of closed self-cross (CS) and closed outcross (CO) treatments on fruit weight and seed number in the greenhouse, in tandem with the field experiments. We randomly selected 24 jalapeño plants for a closed self-cross (CS) and closed outcross (CO) experiment in the greenhouse (12 plants per treatment). In this experiment, closed refers to the fact that insect pollinators were excluded from the plants with mesh bags prior to the treatment and we measured the role of self-pollination on pepper reproduction. In the closed self-cross (CS) treatment, the bag was opened and then one recently opened flower was randomly selected from the plant and hand-pollinated using a sterile q-tip that was rubbed in a circular motion against the anthers of the flower for 8 s, then rubbed on the stigma of the same flower in a circular motion for 8 s (same duration as the closed outcross treatment), and then the bag was closed immediately after the treatment. In the closed outcross (CO) treatment, the bag was opened and then one recently opened flower was randomly selected from the plant and hand-pollinated for 8 s using flowers from donor plants. Specifically, we randomly selected four anthers from two randomly selected pollen donor plants (2 pollen-laden anthers per pollen donor, of the six anthers available per flower). Anthers were removed from the donor flowers using forceps and manually rubbed in a circular motion on the receptive stigma of the closed outcross pollination treatment flower for 2 s each, and then the bag was closed immediately after the treatment. After 48 h the plants were unbagged to allow for unhindered fruit growth after the period of pistil receptivity had passed (Aleemullah et al. 2000; Ofosu-Anim et al. 2006). To further safeguard against any potential insect visitation that might bias our treatments, we maintained the plants in a sterile indoor insect-free greenhouse space for 69 d. We then measured fruit weight (g) and seed number for the fruits in each treatment.

Data analysis

We first evaluated the potential role of local and landscape habitat factors on pollinator abundance and richness. Then, using just the open treatment of the field experiments (those which experienced ambient insect pollination), we evaluated the potential relationship between pollinator abundance and

richness, as well as local and landscape habitat factors, on fruit weight and seed number. Finally, we compared the fruit weight and seed number of the different pollination treatments for the greenhouse and field experiments.

Impacts of local and landscape features on pollinator abundance & richness

We used linear models with the `lm` function in R to examine relationships between local and landscape variables on both number of pollinators (abundance) and pollinator richness, as both pollinator indices met assumptions of normality. Richness for the pollinator communities was calculated using the Chao1 estimator (Chao 1984; Chao 2006) in the `vegan` R package (Oksanen et al. 2016). Chao1 is an extrapolated measure of species richness which accounts for undersampling by estimating higher species richness for samples with more rare taxa present (Chao 1984). We felt this approach was appropriate for our study given substantial variation in pollinator abundance across urban landscapes (as see in Ballare et al. 2019). Because many local and landscape variables were correlated, we prioritized variables previously found to be ecologically meaningful in describing pollinator richness in the same field sites (Quistberg et al. 2016). Using this process, our full model contained four local vegetation predictor variables – mulch, herbaceous plant richness, the number of woody plants, and the number of flowers, as well as one landscape predictor variable – proportion natural habitat cover (in a 2 km radius). The herbaceous plant diversity index included crop, weed, and ornamental species in the garden and was calculated using the Chao estimator. We then ran tests to identify collinearity of predictors in all of our linear models by calculating a variance inflation factor (VIF) for each model set using the `car` package in R (Fox and Weisberg 2018) and ensured that all variables met a VIF cutoff score of 3. We ran model selection using the `MuMIn` package (Barton 2018), an information-theoretic selection process that operates by subsetting the model. A set of models is generated with all possible combinations of the five predictor variables listed above (base model). We selected the top model based on the AICc values. For models where the AICc for top models was within 2 points of the next best model, we calculated model averages (Table S1).

Local, landscape, and pollinator impacts on pollination

Next, we evaluated the impact of these same local and landscape variables on fruit weight and seed number for the open pollination treatments. Because we were interested in evaluating the impact of the interaction between pollinators and their food resources, we included an interaction between the number of pollinators and the number of flowers (number of

pollinators*number of flowers) and the richness of pollinators and number of flowers (richness of pollinators*number of flowers). Our models contained the following predictor variables: number of pollinators*number of flowers, richness of pollinators*number of flowers, mulch, number of woody plants, diversity of herbaceous plant species, and proportion of natural habitat (2 km) as fixed effects. We checked that VIF scores were still below 3 and used a linear model for the fruit weight data using `lm` in the `stats` R package, as fruit weight data met assumptions of normality, and a generalized linear model with a Poisson distribution for the seed number data using `glm` in the `MASS` R package (Ripley et al. 2013), because seed number is count based and was underdispersed for a Negative Binomial distribution. We again ran model selection using the `MuMIn` package (Barton 2013) and selected the top model based on the AICc values. For models where the AICc for top models was within 2 points of the next best model, we calculated model averages. We also ran the same models using bee richness and bee abundance instead of pollinator richness and abundance, and found similar patterns (Table S2). To determine the goodness-of-fit of all best models, we calculated a pseudo- R^2 value as $[(\text{null deviance} - \text{residual deviance}) / \text{null deviance}]$ (Dobson & Barnett 2008).

Greenhouse and field experiments

In the greenhouse experiments we examined if pepper plants are self-compatible and/or enhanced by cross-pollination. To examine how fruit weight was influenced by these two treatment types, we ran a linear model using the `lm` function in the `stats` R package. To examine how seed set was influenced by these treatment two types, we used a generalized linear model with a Poisson distribution using the `glm` function in the `stats` R package. We also compared the means via a post-hoc Tukey test. For the field experiments, we examined if there was a significant difference between the closed treatment (C), open treatment (O), and outcrossed-open (OO) treatment for fruit weight and seed number. Specifically, to examine how fruit weight was influenced by these three treatment types, we ran a linear mixed effect model using the `lmer` function in R with garden as a random effect. For seed number, we used a generalized linear mixed effect model with a Poisson distribution using the `glmer` function also with garden as a random effect. Both analyses were conducted with the `lme4` R package in R (Bates et al. 2015). We then compared means via a posthoc Tukey test.

Results

Local and landscape impacts on pollinator abundance & richness

The taxonomic identities of pollinators observed in this study are described in the supplemental information (Table S3). We

observed 2583 total pollinators visiting flowers. We observed 22 distinct taxonomic groups and an average abundance of 132.83 (± 11.51 SE) individuals and average richness of 9.54 (± 0.59 SE) morphospecies per site. Pollinator abundance was lower where mulch cover was higher ($p < 0.05$, Fig. 3). After averaging the top models ($AIC_c < 2$), mulch was the only significant predictor of pollinator abundance (Table 1b). Pollinator richness (Chao estimator) was not significantly predicted by any local or landscape habitat factor (Table S4a & b).

Local, landscape, and pollinator impacts on pollination

Fruit weight was not predicted by any local or landscape habitat factor or pollinator factor. Seed number increased with number of woody plants ($p < 0.0001$) and herbaceous plant species ($p < 0.0001$), decreased with the proportion of semi-natural habitat in a 2 km radius ($p < 0.0001$), and was unaffected by mulch ($p = 0.834$). We found a positive interaction between pollinator richness and flower number ($p < 0.0001$). When there were more flowers in the garden, the positive relationship between pollinator richness and seed number was steeper (Fig. 4). The model also documents a negative effect of the interaction of number of pollinators and number of flowers ($p < 0.0001$), where the higher the pollinator abundance, the more negative the relationship between number of flowers and seed number ($p < 0.0001$) (Fig. 5). After averaging

the top models ($AIC_c < 2$), the same factors remained significant predictors of seed number (Table 2). We found similar patterns when bee richness and bee abundance were substituted for pollinator richness and abundance in the analysis (Table S2).

Greenhouse and field experiments

Our greenhouse experiment confirmed that jalapeños benefit from outcross pollination. Mean fruit weight was higher in closed outcross (CO) plants (19.69 g \pm 1.12 SE) than for closed self-cross (CS) plants (13.39 g \pm 1.29 SE, $p = 0.0015$). Likewise, mean seed number was higher in closed outcross (CO) plants (83.50 g \pm 11.71 SE) than for closed self-cross (CS) plants (34.60 g \pm 9.28 SE) ($p < 0.0001$).

For plants placed in the field, mean fruit weight was 8.28 g (\pm 1.67 SE), 12.28 g (\pm 2.04 SE), and 16.92 g (\pm 1.32 SE), for the closed treatment (C), open treatment (O), and outcrossed-open (OO) treatment, respectively (Fig. 2). Fruit weight was significantly greater in the OO treatment compared to the C treatment ($p = 0.0005$). Fruit weight was not significantly greater between the O and OO treatment ($p = 0.078$), and not significantly different between the O and C treatments ($p = 0.144$). For these same plants, the mean seed number was 23.84 (\pm 6.60 SE), 39.42 (\pm 12.11 SE), and 48.36 (\pm 8.71 SE) for the closed treatment (C), open treatment (O), and outcrossed-open (OO) treatment, respectively. Seed number was significantly different between all treatment comparisons ($p < 0.0001$).

Table 1 (a) Base linear model of pollinator abundance and (b) best model, calculated as model average of the best three models (all within $\Delta 2AIC_c$, model details in methods). Intercepts are scaled values. (Signif. code: ‘*’ 0.05, ‘**’ 0.01, ‘***’ 0.001)

(a) base lm of pollinator abundance, Poisson distribution				
Coefficients				
	Estimate	Std. Error	T-value	Pr(> t)
Intercept	133.316	9.841	13.547	4.82e-09 ***
Herbaceous Plant Richness	20.439	10.546	1.938	0.075
Natural Cover (2 km)	16.560	10.971	1.509	0.155
Number Woody Plants	-9.027	11.688	-2.572	0.023*
% Mulch Cover	-29.934	11.638	-2.572	0.023
Number of Flowers	-7.343	12.819	-0.573	0.577
(b) best model				
Model-averaged coefficients (full avg.)				
	Estimate	Std. Error	Z-value	Pr(> z)
Intercept	133.316	10.404	11.839	<2e-16 ***
% Mulch Cover	-28.686	11.661	2.291	0.022 *
Herbaceous Plant Richness	9.996	12.119	0.797	0.425
Natural Cover (2 km)	6.289	10.883	0.561	0.575
Number Woody Plants	-2.494	7.059	0.341	0.733
Number of Flowers	-1.302	5.419	0.232	0.816

Discussion

Our findings highlight a critical interaction between floral abundance and pollinator community features, with consequences for pollination services in urban landscapes. First, we found that pollinator abundance was significantly higher in urban gardens with less mulch, but was unaffected by other local and landscape factors. Second, we found that jalapeño seed number was significantly and positively impacted by the interaction between pollinator richness and the number of flowers, where the more flowers there are in the garden, the more positive the relationship between pollinator richness and seed number, likely through increased pollinator functional complementarity. In contrast, we found that gardens with high floral abundance had lower seed number when they supported high pollinator abundance, likely through forager dilution effects on plant reproduction. Finally, we observed that jalapeño plant reproduction was significantly higher for insect-mediated treatments (open and open-outcross treatments) compared to no pollination treatments, and highest in the outcross-pollination treatments.

Table 2 (a) Base generalized linear model of seed number with a Poisson distribution and (b) the single best model (no other models within $\Delta 2$ AICc, model details in methods). Intercepts are scaled values. (Signif. code: ‘*’ 0.05, ‘**’ 0.01, ‘***’ 0.001)

(a) base glm of seed number, Poisson distribution				
Coefficients				
	Estimate	Std. Error	Z-value	Pr(> z)
Intercept	3.273	0.059	55.890	<2e-16 ***
Herbaceous Plant Richness	0.231	0.046	5.052	4.36e-07 ***
Number Woody Plants	0.404	0.057	7.045	1.85e-12 ***
Natural Cover (2 km)	−0.452	0.067	−6.762	1.36e-11 ***
% Mulch Cover	0.015	0.072	0.210	0.834
Number Pollinators: Number Flowers	−0.468	0.078	−6.018	1.77e-09 ***
Number Flowers: Richness Pollinators	0.338	0.056	6.027	1.67e-09 ***
(b) best model				
Coefficients				
	Estimate	Std. Error	Z-value	Pr(> z)
Intercept	3.272	0.058	55.964	<2e-16 ***
Herbaceous Plant Richness	0.234	0.043	5.405	6.49e-08 ***
Number Woody Plants	0.405	0.057	7.058	1.69e-12 ***
Natural Cover (2 km)	−0.445	0.057	7.850	4.17e-15 ***
Number Pollinators: Number Flowers	−0.472	0.076	−6.230	4.66e-10 ***
Number Flowers: Richness Pollinators	0.340	0.056	6.112	9.83e-10 ***

Local and landscape impacts on pollinator abundance & richness

Previous studies have found that garden size, annual floral resources, and woody perennial plants are associated with bee abundance and richness (Quistberg et al. 2016; Matteson and Langellotto 2009). We did not find that floral abundance (which was colinear with garden size in this system) impacted pollinator abundance and richness, possibly because many commonly grown flowers in urban garden systems are not used by pollinators (Lowenstein et al. 2019). However, local groundcover management, specifically, the proportion of soil covered with mulch, was significantly and negatively correlated with pollinator abundance. Mulch was also negatively correlated with pollinator richness, although not significantly. Mulch is negatively associated with the availability of bare soil in many urban gardens (e.g. Quistberg et al. 2016; Ballare et al. 2019), and many bee and non-bee pollinators use bare soil for their nest sites. Previously, in the same study system (Quistberg et al. 2016), a large fraction of the bee community in the study region was comprised of below-ground nesting species (61% of morphospecies), and the abundance of these species was positively correlated with bare ground availability. Our results resonate with past research within this system and in other systems that also find a positive correlation between bare ground availability and urban bee abundance (Frankie et al. 2009; Pardee and Philpott 2014; Ballare et al. 2019), indicating that nesting resource availability can be a critical factor structuring urban pollinator

communities. In other words, our results suggest that urban gardeners may be able to promote pollinator abundance by reserving undisturbed patches of bare soils in their urban gardens.

Local, landscape, and pollinator impacts on pollination

For our open-pollination treatments, pollinator richness was associated with increased seed set, a relationship that is well-documented in previous literature. A diverse community may enhance ecosystem services through functional complementarity (Loreau and Hector 2001, Finke and Snyder 2008, Cardinale et al. 2011), which has been found for pollinator diversity and plant reproduction in rural (Fründ et al. 2013a; Mallinger and Gratton 2014; Martins et al. 2015) and urban (Lowenstein et al. 2015) agricultural systems. This is because diverse pollinator communities exhibit species-specific spatial and temporal variation in floral foraging traits and behavior that likely influence plant reproduction (Hoehn et al. 2008; Pisanty et al. 2015). From the plant’s viewpoint, temporal and environmental variation in pollinator species’ morphology (Larsen et al. 2005; Greenleaf et al. 2007) and behavior (Blüthgen and Klein 2011; Rader et al. 2011; Martins et al. 2015) contributes to complementary effects on pollination. The importance of functional complementarity has been documented for pollination in urban systems comprised of specialist and generalist pollinators (Cane et al. 2006; Pauw 2007).

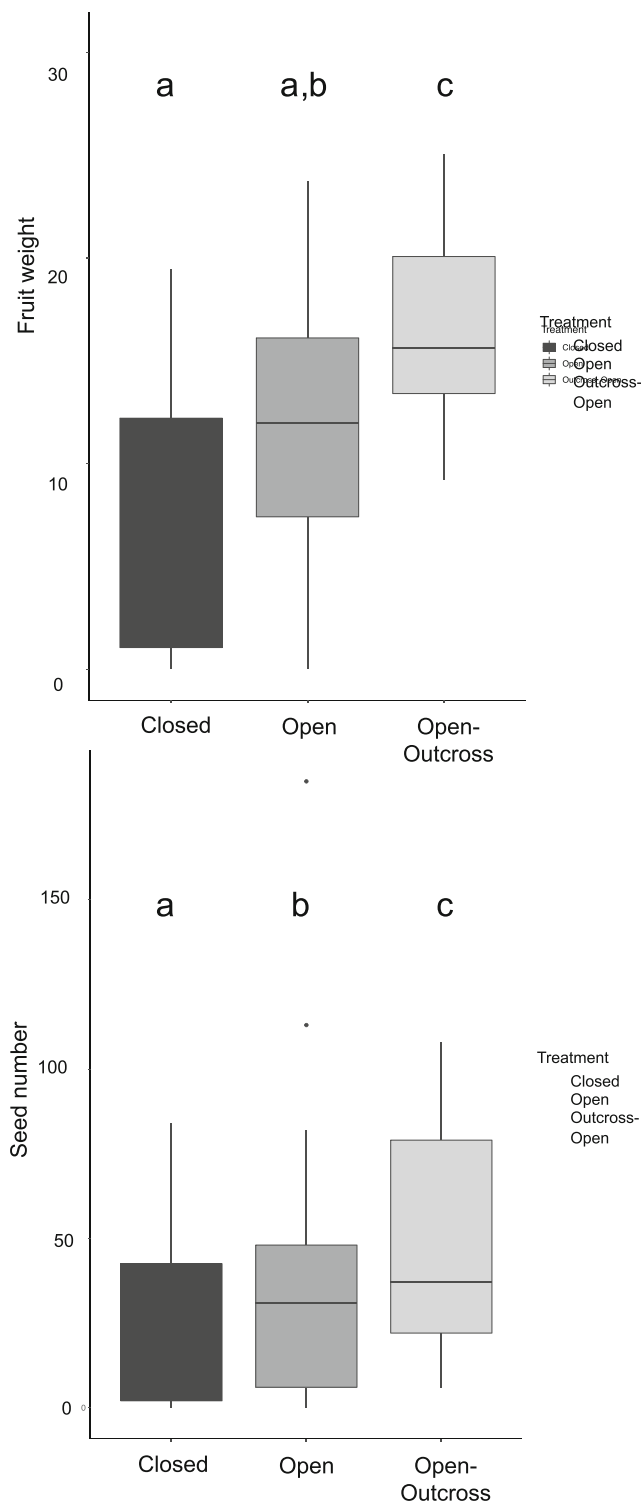


Fig. 2 Box and whisker plots of hand pollination field experiments with resulting (a) Fruit weight and (b) Seed number, where the box is bounded by the 25th and 75th percentile (50th percentile indicated by central horizontal line), the whiskers represent 1.5 x the interquartile range, and the points represent outliers. Boxes with the same letter are not significantly different, while those with no common letters are significantly different ($p < 0.001$)

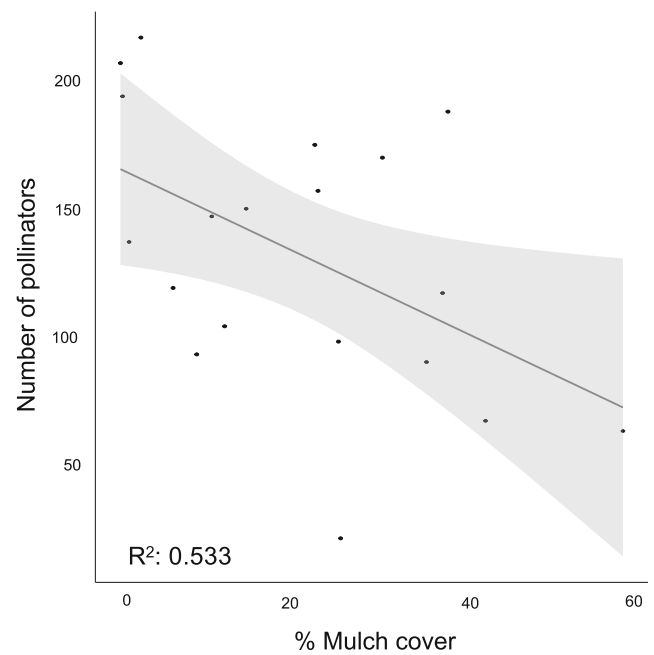


Fig. 3 Mean mulch cover as a predictor of the number of pollinators in a linear model. The shaded area represents the standard errors

Consistent with previous studies in natural (Blaauw and Isaacs 2014b) and urban systems (Potter and LeBuhn 2015; Davis et al. 2017), our study indicates that pollination function is strongly impacted by floral resources in the habitat. We found that the relationship between pollinator richness and seed set became steeper in gardens with high floral abundance. This may be due to impacts of floral resource availability on pollinator foraging behavior. Floral quantity, structure, and diversity at local scales can concentrate pollinator activity (Veddeler et al. 2006) and can influence plant constancy (Kunin and Iwasa 1996), preference (Hambäck 2001), and pollen deposition (Lortie and Aarssen 1999). One methodological limitation to this study is that we relied on visual counts to sample pollinators, which may alter our ability to compare our results with other collection-based pollination studies. For example, Quistberg et al. 2016 collected pollinators with pan traps and netting and reported 55 unique species in this system, whereas we only identified 22 morphospecies, likely because visual surveys often miss rare species (Bosch et al. 2009). However, past studies have found that visual surveys are representative of the pollinator community and can be useful methods when destructive sampling is not possible (Mandelik et al. 2012). Further, past studies have often focused on bees as key pollinators, and while pepper flowers are visited by a wide range of insects, they do benefit from buzz pollination provided by bees (Raw 2000). We therefore modeled the impact of bees on crop seed number and found similar patterns (Table S2). Another caveat to our findings is that study does not distinguish between floral visitors and pollination visits (King et al. 2013), as we do not measure pollen loads or pollen deposition. This may be important

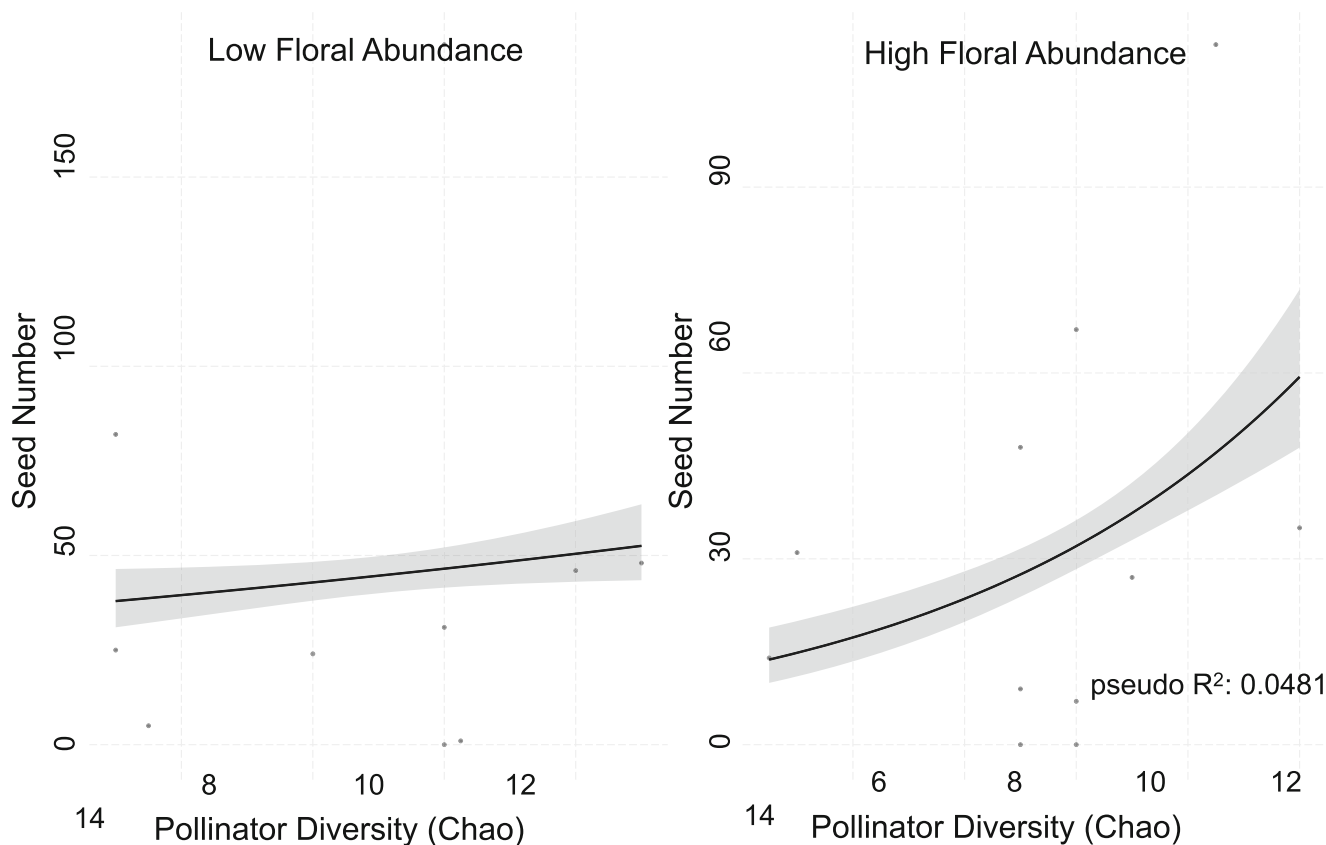


Fig. 4 Impact of the interaction between richness of pollinators and number of flowers on seed number from the glm (Poisson) model. In order to visualize the interaction, the panels represent a split in the data at the average median floral abundance cover across sampling periods

and gardens (41 flowers). The left panel (low floral abundance) represents gardens with less-than or equal to the median number of flowers, the right panel (high floral abundance) represents gardens with more the median number of flowers. The shaded area represents standard errors

because landscape composition and agricultural management can impact pollinator foraging behavior (Moreirra et al. 2015) and may impact resulting pollen deposition (Werrell et al. 2009). However, the benefit of observing all floral visitors, regardless of pollen transfer, is that the diversity of these interaction webs is known to enhance the persistence of plant communities (Fontaine et al. 2005) and inter-specific, indirect interactions have been shown to promote pollination of crops (Greenleaf and Kremen 2006).

While we found that the impact of pollinator richness on seed set becomes stronger in floral-abundant habitats, we found that the impact of pollinator abundance on seed set becomes weaker. This may indicate a per-plant dilution effect in which pollinator densities at flowers decrease in resource-dense patches. This has been previously observed in a prairie system when flower density was increased (Wenninger et al. 2016), possibly due to competition between pollinator individuals in abundant communities of pollinators. The underlying mechanism for why high pollinator abundance without species richness leads to greater competition is likely the same mechanism that promotes co-existence within all communities: intraspecific competition is assumed to be greater than interspecific competition (reviewed in Chesson 2000).

Competition might translate into negative effects on plant reproduction if the energetic costs of foraging are minimized by avoiding competitive interactions at floral sites (Charnov 1976). Additionally, high resource density patches might provide fewer resources for abundant foragers due to saturation effects (Totland and Matthews 1998; Andersson et al. 2013), wherein floral resources attract an abundance of pollinators but there are not enough resources if they all rely on the same pollen and nectar types. Thus, effects to pollination should be more pronounced in low-diversity pollinator communities. While some research has suggested that the presence of dilution effects depends on pollinator species identity and their behavior (Jha and Vandermeer 2009), further research is required to examine how species-specific pollinator foraging traits differentially mediate pollination outcomes across a gradient of resource landscapes.

Our finding that increasing floral resources only mediates plant reproductive success when pollinator richness is high is pertinent because urbanization is associated with increased homogenization of pollinator communities (Deguines et al. 2016; Harrison et al. 2018; Fitch et al. 2019; Wilson and Jamieson 2019). In rural agricultural systems, Kleijn et al. found that a few abundant species provide the bulk of

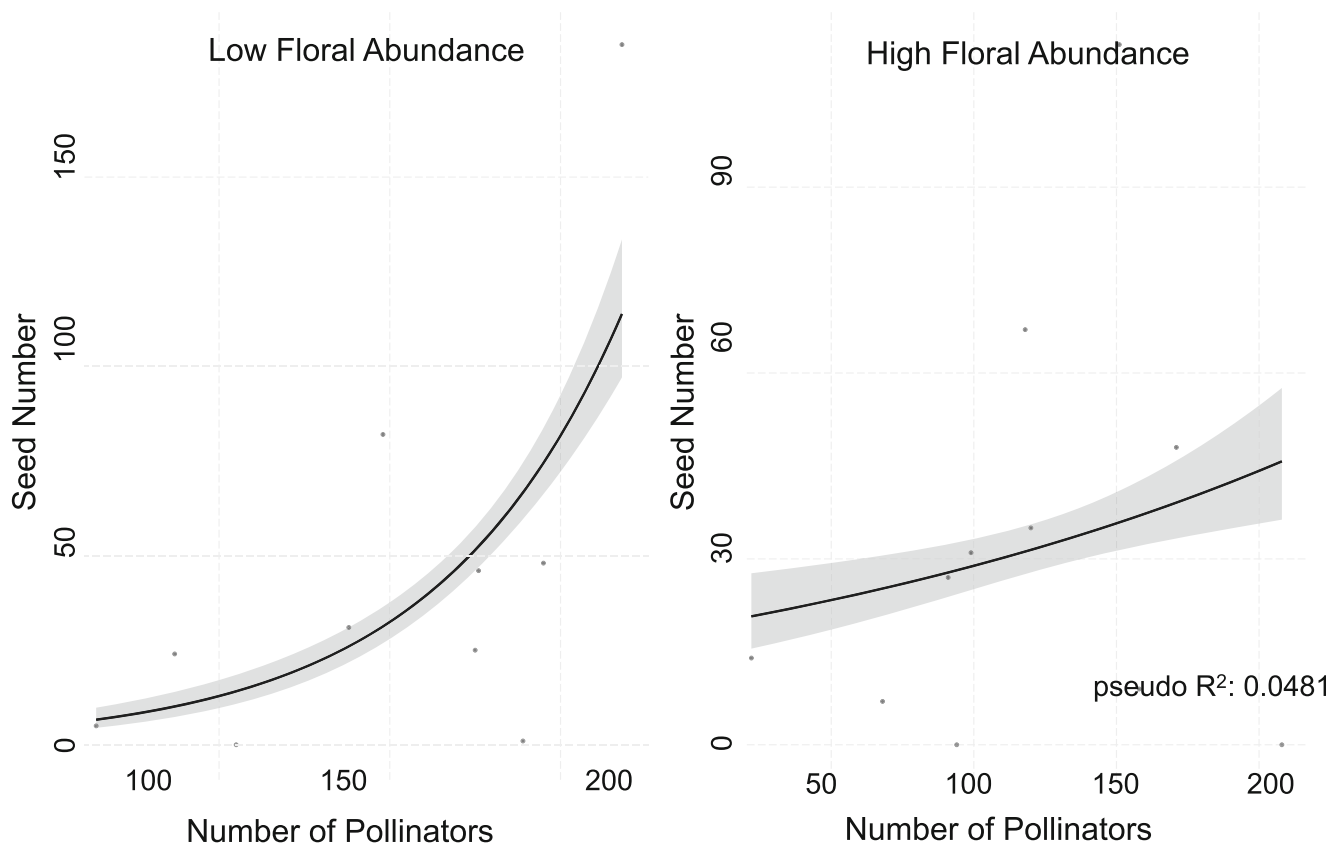


Fig. 5 Impact of the interaction between number of pollinators and number of flowers on seed number from the glm (Poisson) model. In order to visualize the interaction, the panels represent a split in the data at the average median floral abundance cover across all of the gardens (41

flowers). The left panel (low floral abundance) represents gardens with less-than or equal to the median number of flowers, the right panel (high floral abundance) represents gardens with more the median number of flowers. The shaded area represents standard errors

pollination services (Kleijn et al. 2015), but our findings suggest that the importance of pollinator richness likely varies between urban systems and rural agricultural systems, possibly because resource pulses in urban systems are not predictably constrained to seasonable mass-bloom events. Within urban gardens, past studies have shown that pollinator species richness is mostly driven by floral diversity (Plascencia and Philpott 2017), but we did not find this. More research is needed on which species of flowers are most important for bees; Lowenstein et al. found that the composition and identity of flowering resources may be more important than floral abundance for predicting plant-pollinator interactions (2019). Mechanistically, many pollinators require pollen and nectar for calories (Tepedino and Parker 1982) and a greater diversity of pollen has been linked to enhanced pollinator growth rates (Tasei and Aupinel 2008) and pollinator diversity (Petanidou and Vokou 1990). Taken together, these studies indicate that efforts to provision for pollinators with floral plantings will have the greatest impacts on seed set if they also promote species-rich pollinator communities (rather than being dominated by a few, abundant species).

We observed a positive influence of woody plant abundance on pollination function. Many trees and shrubs planted

in urban gardens are fruit-producing with blooms that provide nectar for a diversity of flies, wasps, and bees (Somme et al. 2016). Furthermore, trees and shrubs have been shown to influence bee abundance and richness in past studies (Jha and Vandermeer 2010; Pardee and Philpott 2014), and their abundance in an agroecosystem is often predictive of crop reproductive success (Garibaldi et al. 2013). We therefore were surprised not to find a relationship between woody plants and pollinator richness or abundance. There may be other indirect mechanisms by which trees and shrubs positively impact pollination, for example, by modifying local microclimate (Kilkenny and Galloway 2007). In this system, woody plant availability was colinear with garden size, which Werrell et al. previously found to be important for con-specific pollen deposition on experimental cucumber crops in urban gardens (2009). The availability of woody plants may also influence pollinator behavior (Klein et al. 2004; Williams 2011) and increase overall pollen collection (Dyer et al. 2011). Overall, our study highlights the importance of local habitat conditions when managing for optimal ecosystem function. One possible application of our findings is the suggestion that gardeners plan for a combination of perennial woody plants and annual herbaceous plant species in the garden.

We found that the amount of natural habitat surrounding a garden had a negative effect on seed number. While we had hypothesized that natural cover would enhance beneficial insect movement between crop and non-crop habitat, as seen in many rural landscapes (e.g., Chaplin-Kramer et al. 2011; Klein et al. 2012; Cusser et al. 2016), we did not find this pattern, likely because of our crop selection and the urban landscape. First, our focal crop, the *C. annuum* pepper, is not found in natural habitat fragments, so pollinators recently visiting natural habitat are not likely to carry conspecific pollen. Second, we posit that pollinators in urban landscapes may not always be moving from natural habitat into gardens. Third, given the challenges of traversing private property surrounding the gardens, we could not ground-truth to verify the landcover data for the region. Indeed, past studies in our study system have found that natural habitat cover does not have the expected positive impact on pollinator abundance and richness (Quistberg et al. 2016) or pest-control provision (Egerer et al. 2017). These findings corroborate those of Gaines-Day and Gratton (2016), which indicate that wild bees may prefer to remain locally when surrounded by less hospitable landscapes. In another study of urban gardens in New York City, Matteson & Langellotto found that 45% of marked bumble bee individuals were later collected in the gardens where they had initially been documented, indicating that bumble bees, otherwise long-distance foragers, may largely forage within a single garden in urban areas (Matteson and Langellotto 2009). Based on the findings and other similar intensely managed landscapes, it is possible that within-garden habitat features may play a disproportionately large role in mediating pollinator foraging and nesting patterns in urban landscapes.

Greenhouse and field pollination experiments

For both the greenhouse and field-based experiments, jalapeño seed number was significantly higher in open-outcross treatments than in open treatments or closed treatments. This finding highlights the importance of insect pollinators for enhancing the reproduction of crops like jalapeño peppers, however, gardeners likely benefit more from increased fruit weight than seed number. We found that fruit weight followed similar patterns but was not significantly different between treatments, possibly because fruit is largely comprised of maternal tissue and can reach maximum weight in peppers even when seed number is low (Marcelis 1997). Furthermore, to assess fruit weight we measured wet weight, not dry weight. While plants were watered in a standardized manner under homogenous greenhouse conditions, it is possible that slight differences in watering could influence fruit weight data. We found that the fruit weight and seed number of plants grown in greenhouse conditions (across all treatments) were higher than those grown in the field, perhaps due to the optimal climate conditions provided by greenhouses for peppers (Bakker 1989; Shaked et al. 2004; Pagamas and Nawata 2008).

Conclusions

Animal-mediated pollination is critical for the majority of flowering wild plant species (Ollerton et al. 2011) and within agricultural systems, where more than 75% of domesticated crops show increases to fruit or seed set (Klein et al. 2006). In this study, we add to the body of literature suggesting that insect pollination is an essential part of successful plant reproduction in urban systems (Verboven et al. 2014, Leong et al. 2014, Lowenstein et al. 2015, Potter and LeBuhn 2015). Furthermore, while resource-driven foraging interactions have been documented to impact pollinator visitation in simulated models (Essenberg 2012), grasslands (Totland and Matthews 1998) floodplains (Ebeling et al. 2008), and rural agricultural systems (Veddeler et al. 2006; Jha and Vandermeer 2009; Evans et al. 2017; Xie et al. 2019), our study is the first to document this interaction mediating plant reproduction within urban landscapes. Specifically, we show that when urban garden floral density is high, increasing pollinator richness (and not pollinator abundance) increases crop reproductive success. In other words, our study indicates that local pollinator foraging interactions can significantly influence ecosystem service provision. To achieve optimal pollination services in their urban gardens, more research is needed to identify which practices optimize for both pollinator richness and floral resource availability.

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Authors' contributions HC participated in study design, participated in fieldwork, conducted data analysis, and coordinated manuscript writing and publication. SMP acquired funding for the project, participated in study design, fieldwork logistics, and manuscript writing. BBL and HL acquired funding for the project, participated in study design, and manuscript writing. SJ acquired funding for the project, coordinated the study and participated in study design, field work, data analysis, and manuscript writing and publication. All authors gave final approval for publication.

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Compliance with ethical standards

Declaration of interest none.

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