

# Urbanization-mediated context dependence in the effect of floral neighborhood on pollinator visitation

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**Abstract** Context dependence in ecological interactions is widespread, but our ability to predict how environmental variation will mediate the effects of a given interaction remains poor. Co-flowering plants can influence visitation of shared pollinators to one another; the effect of these interactions varies with ecological context. While research has investigated the effect of local biotic conditions on such interactions, little is known about how land use change, specifically urbanization, affects them. I tested how the interaction of urbanization and neighborhood floral density (NFD) and richness affected pollinator visitation rates to two crop species, cucumber and sunflower by placing experimental arrays of each species in paired high- (garden) and low- (lawn) floral density neighborhoods along an urban-to-rural gradient. Pollinator visitation to flowers was monitored over 2 years, as was NFD and richness. The two plant species showed contrasting responses to both urbanization and floral neighborhood density, with only cucumber experiencing context dependence in the effect of floral neighborhood. These contrasting responses to urbanization and floral neighborhood are likely due to differences between species in floral visitor community composition. Plants grown in gardens experienced higher pollinator visitation regardless of floral neighborhood. This study highlights the need for

better understanding of genus- or species-specific pollinator responses to urbanization to predict the effect of urbanization on plant–pollinator interactions.

**Keywords** Contingency · Facilitation · Pollinator-mediated plant interactions · Urban ecology · Floral neighborhood effects

## Introduction

The effect of a biotic interaction on participating organisms can vary in both magnitude and direction depending on the broader ecological context in which the interaction occurs. Such context dependence is widespread in ecological interactions (Chamberlain et al. 2014), and can be generated by variation in either abiotic conditions (Callaway et al. 2002; Juliano 2009) or the biotic community (Moeller 2004; Schadler et al. 2007) across both space and time. Despite recognition of the pervasiveness of context dependence in ecological interactions, our ability to predict how particular environmental variation will mediate the effects of a given interaction remains poor (Agrawal et al. 2007; Chamberlain et al. 2014). This is particularly problematic, given the extent to which anthropogenic activities are altering environmental conditions; an understanding of how human-induced changes to ecosystems might impact species interactions is crucial to our ability to maintain ecosystem function and services in the face of rapid change.

A key source of anthropogenic environmental impact is land use change, particularly agricultural conversion or intensification and urbanization. The effects of agriculture-associated environmental change on species interactions have been documented for multiple interaction types, including competition (Perfecto and Vandermeer 1996), herbivory

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(Hahn and Orrock 2015), parasitism (Tylianakis et al. 2007), and mutualism (Cariveau et al. 2013). Yet there exists very little work documenting similar effects from urbanization (but see Hennig and Ghazoul 2011; Farwell and Marzluff 2013). Given the rapidly increasing extent of urban areas worldwide (Seto et al. 2012), this represents a crucial knowledge gap.

The need to understand how changing environmental context might affect plant–pollinator interactions is particularly urgent. Globally, 87% of plant species (Ollerton et al. 2011) and nearly 35% of all crop production (Klein et al. 2007) depends on animal pollinators. At the same time, pollinator populations are in decline in many areas (Potts et al. 2010), prompting widespread concern about the continued provisioning of pollination services at levels necessary to maintain agricultural yields (Klein et al. 2007; Koh et al. 2016) and native plant communities (Biesmeijer et al. 2006; Vamosi et al. 2006). Pollinator responses to urbanization in particular are complex and often variable across pollinator taxa (Cane et al. 2006; Matteson and Langelotto 2010; Lowenstein et al. 2014). Moreover, the causal mechanisms linking urbanization, pollinator community shifts, and pollination effectiveness remains poorly understood (Harrison and Winfree 2015). One outstanding question in this area is whether urbanization affects the outcome of interactions for pollination among co-flowering plants that share pollinators.

Most pollinators exploit floral resources from a range of plant species (Waser et al. 1996; Johnson and Steiner 2000), which can lead to competition for pollination among co-flowering plants that share pollinators (Rathcke 1983). Competitive effects can arise either from reductions in pollinator visitation resulting from the greater abundance of alternative floral resources (Kunin 1997; Ghazoul 2005), or reduced pollination effectiveness as a result of increased heterospecific pollen transfer (Ghazoul 2005; Morales and Traveset 2008). But competition is not inevitable in pollinator-mediated plant–plant interactions. Rather, these interactions occur along a continuum from competition to facilitation, depending on the context in which the interactions occur (Rathcke 1983; Feldman et al. 2004). Facilitation is likely when the focal species occurs at low densities and, as a result, fails to attract sufficient pollinators to achieve adequate pollination (Rathcke 1983; Feldman et al. 2004). In such a situation, co-flowering heterospecifics in the neighborhood of individuals of the focal species can increase pollinator attraction sufficiently to result in per-plant increases in pollination of that species. Such context-dependent facilitation can result from either an aggregative response of pollinators to floral density, i.e., a larger floral display attracts disproportionately more pollinators than small displays—or an accelerating functional response of individual pollinators as floral density increases (Feldman 2006). In either case, at some floral density, pollinator response asymptotes, and the

relationship with co-flowering heterospecifics shifts towards competition (Rathcke 1983; Feldman et al. 2004; Feldman 2006). Facilitative effects of floral neighborhood have been demonstrated in a range of habitats and plant types (Moeller 2004; Ghazoul 2006; Ye et al. 2014; Tur et al. 2016).

To date, most studies examining the effects of floral neighborhood on pollinator visitation have occurred in natural habitats, and there has been no explicit test of whether urbanization affects pollinator-mediated interactions among co-flowering plants. What little work has occurred in urban areas, however, suggests that urbanization may increase the strength of competition in pollinator-mediated plant–plant interactions. For example, Hennig and Ghazoul (2011) found that visitation to *Trifolium pratense* L. (Fabaceae) in urban green spaces declined as neighborhood floral density (NFD) and diversity increased, even in patches where the density of *T. pratense* was low enough to result in facilitative effects of floral neighborhood in a similar study (Ghazoul 2006) conducted in a rural landscape. This suggests that urbanization may influence plants' interaction for pollination differently than other landscape modifications through distinctive effects on, for example, pollinator community composition (Fortel et al. 2014; Harrison and Winfree 2015), pollinator foraging (Andrieu et al. 2009), or pollinator movement (Jha and Kremen 2013). Moreover, because pollinators exhibit diverse responses to urbanization (Cane et al. 2006; Banaszak-Cibicka and Żmihorski 2011; Fortel et al. 2014), it seems likely that the effects of urbanization on pollination will likewise be uneven across plant species.

In this study, I evaluated the effect of two distinct but interacting environmental gradients—NFD and urban development—on pollinator visitation to two plant species, cucumber (*Cucumis sativus* L., Cucurbitaceae) and common sunflower (*Helianthus annuus* L., Asteraceae), to determine if and how urbanization alters the effect of floral neighborhood on pollinator visitation. I predicted that pollinator visitation would decline with urbanization, and that, moreover, urbanization would exacerbate competition for pollination. I predicted that this context dependence would be more pronounced for *C. sativus*, which is less attractive to generalist pollinators than *H. annuus* (Delaplane and Mayer 2000), and therefore, more sensitive to the effects—whether positive or negative—of floral neighborhood.

## Methods

### Paired experimental gardens along urban-to-rural gradient

In 2014, I established 10 paired experimental plots, 2 each at 5 locations along an urban-to-rural gradient in SE Michigan, USA; the same plots were used again in 2015. For each

location, one plot was located within a community garden and the other nearby in an area of comparable urbanization but outside a garden. Non-garden plots were all located in patches of lawn, though lawn size varied across plots. I expected gardens to have higher floral density than paired lawns, and therefore, that this paired design would provide plots with low- and high-density floral neighborhoods while controlling for urbanization. Distance between paired plots ranged from 144 to 700 m; distance between locations ranged from 6 km to 67 km (Supplementary Table 1). Locations were chosen to cover the range of development intensity found in the region, but were constrained to areas with community gardens. Paired plots were matched for degree of solar exposure, with all plots having southern exposure.

Each experimental plot included three individuals each of *C. sativus* and *H. annuus*, with plants of each species arranged in a triangle. These species are both commonly cultivated in community gardens in SE Michigan (G. Fitch unpublished data).

Plants were grown from seed in 5-gal plastic nursery pots filled with a mixture of 3 parts organic potting soil (SUGROM 1.5; Sun Gro Horticulture, Agawam MA) to one part organic compost (derived from plant materials; mixed and incubated from on-site material at the University of Michigan Matthaei Botanical Gardens). All plants were kept in standard greenhouse conditions until the onset of flowering, at which point they were relocated to randomly assigned plots. At each plot, pots were sunk into the ground so that the rim of the pot was flush with the top of the soil. All pots were mulched with straw to a depth of 4 cm, and a drip-watering device was installed in each pot to reduce the necessary frequency of watering. I installed galvanized steel tomato cages (Gilbert & Bennett; MAT Holdings Inc., Long Grove, IL) around cucumber plants to support their growth and encourage trellising. Plants were watered as needed at each visit. There was no early season plant mortality, but several *C. sativus* individuals succumbed to cucumber bacterial wilt in early August 2014; because this was after peak flowering for these plants, dead plants were not replaced.

### Pollinator visitation

Between 28-Jun and 6-Sep-2014 and 26-Jun and 21-Aug-2015, I visited each plot approximately twice per week (no more than 1 visit every 3 days) while flowering was in progress to observe pollinator visitation to experimental plants. Observations occurred between 0900 and 1600 on days when the sky was sunny or brightly overcast, temperatures exceeded 20 °C, and average wind speed was < 2 m/s at 1 m above the ground, with gusts of no more than 5 m/s. On each visit, I recorded the number and sex of all *C. sativus* blossoms and the number of *H. annuus* inflorescences in bloom. I then observed the plants for 30 min, recording all

pollinator visits to the focal plants. Any insect seen in contact with the reproductive parts of a floral unit was recorded as a visitor, though ants (Hymenoptera: Formicidae), which accounted for < 2.5% of visits to either species, were subsequently removed from the dataset prior to analysis because ants are generally considered to be poor pollinators (Beattie et al. 1984; Dutton and Frederickson 2012, though see, e.g. Gómez and Zamora 1992). Multiple visits by the same individual, whether to one or multiple floral units, were counted as distinct visits, except in cases where the insect was seen leaving and then returning to the same floral unit without an intervening visit to another floral unit, in which case only the first visit was counted. Flower visitors were identified to morphospecies. If a visitor could not be assigned to morphospecies, it was collected for later identification once it left the floral unit. Specimen identifications were made using the Discover Life online key (Ascher and Pickering 2016), with the identification of voucher specimens verified by J. Gibbs. Specimens are housed in the University of Michigan entomological collections.

To assess floral richness and density, on each visit to a plot I conducted floral surveys. During each survey, I identified all potentially pollinator-attracting flowers (i.e. all flowers excluding those that were wind-pollinated, except in cases where pollinators were clearly attracted to pollen on wind-pollinated flowers) blooming within 20 m of a point at the center of the experimental plant array and, for each species in flower, counted the number of floral units. A floral unit comprised either individual flowers or, in species where individual flowers were small (< 1 cm in diameter) and densely packed in inflorescences (e.g. many Asteraceae), as individual inflorescences. Total floral density is thus the sum of all floral units in bloom at the time of the survey, divided by the survey area in m<sup>2</sup>. Where individuals could not be identified to species, I photographed and/or collected samples to be used for later identification.

### Land cover data

Land cover was analyzed using data from the National Land Cover Database (NLCD; Homer et al. 2015) with ArcGIS (Esri, Redlands, CA). To assess degree of urbanization, a collaborator (Maria Carolina Simao) the percent of 30 m × 30 m cells classified as ‘developed, medium intensity’ and ‘developed, high intensity’ within a circle centered on the experimental plants and varying in radius from 500 to 2500 m in 500 m increments. A GLMM with Poisson distribution and logit link (R package lme4, function glmer) was used to determine which radius had the greatest effect on visitation rates; response variable was the number of pollinator visits to focal plants, with log<sub>10</sub>(number of flowers on experimental plants) included as an offset, and I included plot nested within location as a random effect. Using the

offset allowed me to investigate per-flower rate of visitation while avoiding the complications of using a rate as the response variable. Results indicated that visitation rates to both plant species were best predicted by the 1 km radius, so that radius was used in all subsequent analyses of the effect of urbanization on visitation.

### Statistical analyses

All analyses were carried out in R v.3.3.0 (R Core Team 2016). Total visitation and bee-only visitation were analyzed separately, but because the responses of the two groups were qualitatively similar, only total pollinator visitation is reported here.

ANOVA were used to compare floral neighborhood metrics (total neighborhood floral density and species richness) across plots, to test the expectation that floral resource availability would be greater in within-garden plots. Where ANOVA revealed significant differences, I conducted post hoc analysis using Tukey's HSD test. Correlations between floral richness and density were measured with a linear model. To test whether floral neighborhood metrics were affected by urbanization, I used LMMs with floral metric as the response variable, random variable as described above, and plot type  $\times$  degree of urbanization as predictors. To test the effect of measured covariates—including date, year, and time of observation, and temperature and wind speed at time of observation—on pollinator visitation to each species, I used GLMMs with distribution, link function, response variable, random variable, and offset as described above. In both cases, I created a set of candidate models using stepwise elimination of predictor variables, starting with the maximal model. From these candidate models, I determined the best model by comparison of  $AIC_c$  values and weights.

To test for the effect of floral neighborhood, degree of urbanization, and interaction between floral neighborhood and urbanization on pollinator visitation, I again used GLMMs with Poisson distribution and logit link. Response variable, offset, and random effect were as described above for the models determining the appropriate radius at which to consider land cover. Separate models were constructed for visitation to *C. sativus* and *H. annuus*. Three measures of floral neighborhood were considered, though because of strong collinearity among them, only one was included in a given model: total NFD, confamilial NFD, and total richness. Both measures of NFD were included because (1) pollinator species tend to visit related plants (Vamosi et al. 2014), and therefore, related plants might be more likely to affect visitation, but (2) both plant species studied here are visited by a range of pollinators that may differ in their tendency to visit related plants. For each species, maximal models included year, plot type (garden/non-garden), floral

neighborhood metric (total NFD, confamilial NFD, or total richness), degree of urbanization, and floral metric  $\times$  urbanization interactions as fixed effects. Date of observation was included as a fixed effect in models of visitation to *C. sativus* only, while temperature was included for *H. annuus* only, since preliminary data analysis indicated responses to those variables in only one species (see “Results”). To allow meaningful comparison of parameter estimates, all continuous predictor variables were scaled by subtracting the mean and dividing by the standard deviation. Model evaluation was conducted as described above.

Models were checked for overdispersion using parametric bootstrapping (Harrison 2014). Because overdispersion was initially estimated at  $> 1.4$  for all models, I added an observation-level random effect, which has been shown to be a robust means of accounting for overdispersion in GLMMs of ecological data (Harrison 2014); this reduced the overdispersion parameter estimate to  $< 1.4$  for all models, however, also resulted in convergence failure for some models. When a model failed to converge, I re-started the model from the previous fit and increased the number of iterations; in all cases these changes resulted in model convergence.

Because the response of pollinator visitation to NFD is likely to be nonlinear, I additionally investigated the effect of changing floral density in low-density floral neighborhoods. This analysis included only observations made when NFD was less than 6 floral units  $m^{-2}$ , the threshold chosen because (1) it included sufficient observations from low-density neighborhoods to conduct analyses and (2) visual inspection of plots of pollinator visitation against NFD indicated a peak in visitation rates to plants in plots with floral neighborhoods of this density. This subset included observations from all but one plot that consistently had high-density floral neighborhood. Fixed and random effects in these models are as described above.

Because there was a significant effect of NFD  $\times$  urbanization interaction on visitation to *C. sativus* (see “Results”), to further investigate how urbanization mediated the effect of floral neighborhood I created separate models for visitation to urban and non-urban plots. I define urban plots as those that have  $> 35\%$  developed land within 1 km, a threshold consistent with other studies (e.g., Raciti et al. 2012); this category included 4 plots, while there were 6 non-urban plots. Model construction and selection proceeded as above.

To determine whether (1) visitor community composition differed significantly between *C. sativus* and *H. annuus* and (2) degree of urbanization and plot type affected visitor community composition within each species, I used the function `adonis()` in R package `vegan` (Oksanen et al. 2016) to conduct permutational ANOVA. Because the community of flower visitors differed between the two species, and because of contrasting effects of both urbanization and floral



neighborhood on pollinator visitation to the two plant species (see “Results”), I also examined how urbanization and NFD related to visitation by the most frequent flower visitors to each species. As above, these analyses were conducted using GLMMs, with the response variable the count of visits by the pollinator morphospecies of interest. Offset and random effects were as described above; degree of urbanization, NFD, urbanization  $\times$  NFD interaction, and plot type were included as fixed effects.

## Results

### Plot characteristics

The percentage of medium- or high-intensity development within 1 km of the experimental plot ranged from 5.1 to 99.1% (Suppl. Table 1). Paired garden/non-garden plots at a given site differed in percentage of developed land at this radius by at most 2.8%.

Both floral density and richness varied significantly across plots, and the two measures were positively correlated ( $R^2 = 0.39$ ,  $F_{1,188} = 121.7$ ,  $p < 0.001$ ; see Suppl. Table 2 for an occurrence list of all documented plant species). Neighborhood floral density (NFD) was significantly higher in garden than paired non-garden plots at all locations except the single rural location, where NFD was only marginally higher within the garden (Suppl. Figure 1A). By contrast, species richness was significantly higher in gardens at all locations (Suppl. Figure 1B). Floral density within plots also varied substantially across the period of observation. Degree of urbanization was not a significant predictor of NFD, but had a positive effect on neighborhood floral richness (Suppl. Table 3). The best model for predicting floral richness also included the interaction between degree of urbanization and plot type, indicating that while richness within gardens increased with urbanization, in non-garden plots it decreased (Suppl. Table 3).

### Pollinator visitation

I spent in total 55.5 h observing pollinator visitation to *C. sativus* and 41.5 h observing *H. annuus*. A total of 2719 flower visits were observed over the course of the study—1884 in 2014 and 835 in 2015. Of these, 1311 (48%) were to *C. sativus*, with the remaining 1408 to *H. annuus*. Bees were the most frequent visitors, making 92% of all visits to *C. sativus* and 95% of visits to *H. annuus*. Other visitors included syrphid flies (5% and < 1%, respectively), other dipterans (< 1% and 5%), and small numbers of lepidopterans, coleopterans, and hemipterans. Per-flower visitation rates were variable within plots across observations and

among plots, but were significantly higher for *H. annuus* ( $10.2 \pm 1.2$  (mean  $\pm$  s.e.) visits flower<sup>-1</sup> h<sup>-1</sup>) than *C. sativus* ( $2.0 \pm 0.2$  visits flower<sup>-1</sup> h<sup>-1</sup>; Wilcoxon rank sum test,  $W = 0$ ,  $p < 0.001$ ).

Of environmental covariates, wind speed had no effect on visitation to either species (*C. sativus*:  $z = 1.40$ ,  $p = 0.16$ ; *H. annuus*:  $z = 0.52$ ,  $p = 0.61$ ); temperature had no effect on visitation to *C. sativus* ( $z = 1.36$ ,  $p = 0.17$ ), but was negatively related to visitation to *H. annuus* ( $z = -2.52$ ,  $p = 0.01$ ). Date of observation had a significant positive effect on visitation to *C. sativus* ( $z = 4.04$ ,  $p < 0.001$ ) but no effect on *H. annuus* ( $z = 1.64$ ,  $p = 0.10$ ). In addition, visitation rates to both species were lower in 2015 than 2014 (*C. sativus*:  $z = -1.86$ ,  $p = 0.06$ ; *H. annuus*:  $z = -3.30$ ,  $p < 0.001$ ). Ultimately, date of observation was the only covariate included in the model for visitation to *C. sativus*; temperature and year were included in the best model for *H. annuus*.

**Table 1** Drivers of pollinator visitation to *C. sativus* and *H. annuus*. GLMMs with Poisson distribution and log link

Focal species	<i>C. sativus</i>	<i>H. annuus</i>
Fixed effect	Estimate, <i>P</i>	Estimate, <i>P</i>
<i>(a) All observations</i>		
Degree of urbanization	+ 0.21, 0.07	– <b>0.35, 0.045</b>
Neighborhood floral density (NFD)	– 0.17, 0.11	NA
Asteraceae NFD	NA	– <b>0.30, 0.01</b>
Degree of urbanization $\times$ NFD	– <b>0.29, 0.007</b>	NA
Plot type (garden)	+ <b>0.72, 0.006</b>	+ <b>0.72, &lt; 0.001</b>
Date	+ <b>0.42, &lt; 0.001</b>	NA
Temperature	NA	– 0.16, 0.5
Year	NA	– <b>0.60, 0.004</b>
<i>(b) Observations from low-density floral neighborhoods only</i>		
Degree of urbanization	+ <b>0.41, 0.005</b>	NA
NFD	+ <b>0.33, 0.01</b>	NA
Plot type (garden)	NA	+ <b>0.88, 0.02</b>
Date	+ <b>0.42, &lt; 0.001</b>	NA
Temperature	NA	– 0.12, 0.43
Year	NA	– <b>0.60, 0.04</b>

Response variable is total number of pollinator visits, with log(focal plant flower #) included as offset. Random effects were: (1|location/plot) + (1|id), where id is an observation-level variable introduced to eliminate overdispersion. Neighborhood floral density (NFD) refers to total floral density (# floral units m<sup>-2</sup>) within a 20 m radius of focal plants. Degree of urbanization (DU) is measured as % high- or medium-intensity development within 1 km of the plot. NA indicates that a variable was not included in the best model. Boldface indicates significant effects

a: all observations; b: observations only from low-density floral neighborhoods (< 6 floral units m<sup>-2</sup>)

**Table 2** Comparison of goodness-of-fit for candidate GLMMs of pollinator visitation to *C. sativus* and *H. annuus*

Candidate model—fixed effects	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
<i>C. sativus</i> —all observations		
<b>Neighborhood floral density (NFD) × degree of urbanization (DU) + plot type + date</b>	745.2	0
DU + plot type + date	747.2	1.9
NFD + DU + plot type + date	748.8	3.6
Neighborhood floral richness × DU + plot type + date	749.1	3.9
Cucurbitaceae NFD × DU + plot type + date	751.8	6.6
<i>C. sativus</i> —low-density floral neighborhoods only		
<b>NFD + DU + date</b>	491.0	0
<b>NFD × DU + date</b>	491.6	0.6
NFD + DU + plot type + date	493.4	2.4
DU + date	494.3	3.3
Neighborhood floral richness + DU + date	494.6	3.6
Cucurbitaceae NFD + DU + date	496.8	5.8
<i>H. annuus</i> —all observations		
<b>Asteraceae NFD + plot type + temp + year</b>	584.3	0
<b>Asteraceae NFD + DU + plot type + temp + year</b>	584.5	0.2
Asteraceae NFD × DU + plot type + temp + year	586.4	2.1
NFD + plot type + temp + year	587.1	2.8
Neighborhood floral richness + DU + plot type + temp + year	589.6	5.3
Asteraceae NFD + plot type + year	596.1	11.8
<i>H. annuus</i> —low-density floral neighborhoods only		
<b>Plot type + temp + year</b>	393.3	0
Asteraceae NFD + DU + plot type + temp + year	394.6	1.4
DU + plot type + temp + year	395.8	2.5
Asteraceae NFD × DU + plot type + temp + year	397.7	4.4
NFD + DU + plot type + temp + year	397.8	4.5

Response variable, random effects, and abbreviations as for Table 1. Boldface indicates the best model, as determined by AIC<sub>c</sub> value; multiple models are bolded where ΔAIC<sub>c</sub> < 1

### GLMM analysis: effect of floral neighborhood and urbanization on pollinator visitation

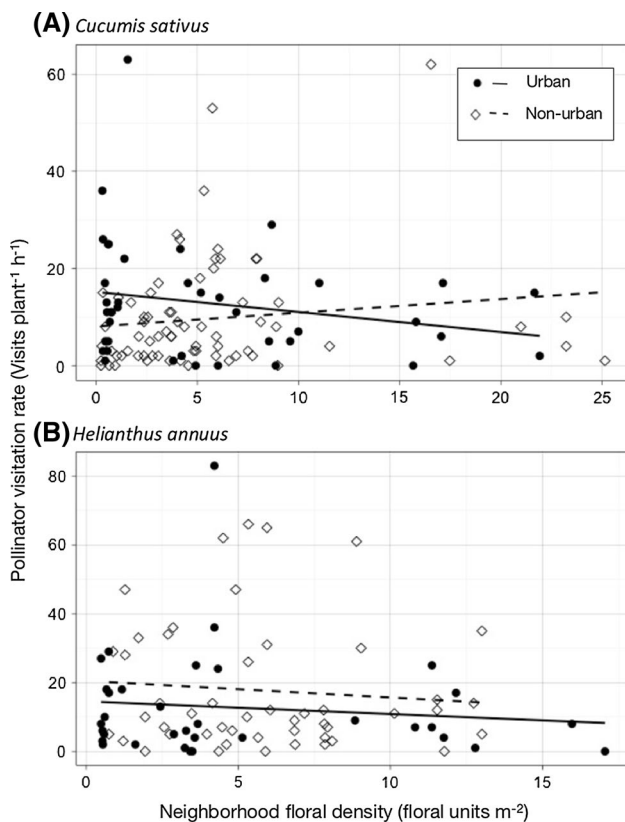
#### Cucumber (*C. sativus*)

Total neighborhood floral density (NFD) was a better predictor of pollinator visitation than either floral species richness or density of only confamilial flowers (Table 2), but nevertheless had only a marginal negative effect on visitation (Table 1a). While pollinator visitation to *C. sativus* responded positively to urbanization, there was a significant, negative NFD × urbanization interaction (Table 1a). When only observations from low-density floral neighborhoods were considered, NFD had a significant positive effect on pollinator visitation (Table 1b); while the sign and magnitude of the NFD × urbanization interaction term was similar to that for the model considering all observations ( $-0.19 \pm 0.13$ ,  $p = 0.13$ ), it was omitted from the best model (Table 2). This omission of the interaction term may be due in part to the lack of observations from low-density floral neighborhoods at the most rural location—where NFD

was consistently moderate to high in both garden and non-garden plots (Suppl. Figure 1A)—reducing the ability to detect a NFD × urbanization interactive effect on pollinator visitation.

Visual inspection of cross-sectional plots illustrating the NFD × urbanization interaction suggested that this effect might be an artifact of a single observation of very high visitation rates to a plot with high NFD and moderate urbanization. However, model diagnostics did not indicate that this observation had undue influence on the overall model fit, and removing the observation had minimal effect on model estimates (Suppl. Table 4).

The negative response to the NFD × urbanization interaction term indicates that in urban sites, increasing NFD disproportionately depressed visitation rates. Consistent with this interpretation, when urban and non-urban plots were considered separately, NFD had a negative effect on visitation in urban plots ( $-0.61 \pm 0.30$ ,  $p = 0.04$ ), while in non-urban plots there was no relationship between floral density and pollinator visitation ( $0.03 \pm 0.12$ ,  $p = 0.76$ ; Fig. 1a). Moreover, the facilitative effect of floral neighborhood



**Fig. 1** Effects of neighborhood floral density on pollinator visitation to **a** *Cucumis sativus* and **b** *Helianthus annuus* in urban versus non-urban plots. Observations from urban plots are represented by filled circles; observations from non-urban plots by open diamonds. Trend lines are according to GLMM analysis: solid line is for urban plots and dashed line for non-urban plots

at low floral densities only obtained in non-urban plots ( $0.40 \pm 0.15$ ,  $p = 0.006$ ); in urban plots there was no relationship between floral density and visitation in low-density floral neighborhoods ( $-0.07 \pm 0.24$ ,  $p = 0.77$ ).

Plot type had a large effect on pollinator visitation, with *C. sativus* in gardens receiving more pollinator visits than those in non-garden plots (Table 1a); though this effect disappeared when only low-density floral neighborhoods were considered (Table 1b).

#### Sunflower (*H. annuus*)

In contrast to *C. sativus*, pollinator visitation to *H. annuus* was better predicted by the density of confamilial blooms rather than total floral density (Table 2); discussion of floral density below, therefore, refers to density of Asteraceae blooms. Visitation to *H. annuus* was significantly negatively affected by NFD (Table 1a). Increasing urbanization depressed pollinator visitation to *H. annuus* (Table 1a),

though the model that omits degree of urbanization is nearly indistinguishable from that which includes it, indicating that this effect is negligible (Table 2). There was no significant floral neighborhood  $\times$  urbanization interaction, and this term was omitted from the best model (Table 2). When only observations from low-density floral neighborhoods were considered, neither NFD nor degree of urbanization were included in the best model (Table 2). As with *C. sativus*, visitation rates were higher in garden than non-garden plots (Table 1a).

#### Pollinator-specific responses to urbanization

While *C. sativus* and *H. annuus* shared many visitors, they differed significantly in visitor community composition ( $R^2 = 0.06$ ,  $F = 12.60$ ,  $p < 0.001$ ; Table 3). The most frequent visitors to *C. sativus* were *Ceratina* sp. (including *C. calcarata*, *C. dupla*, and *C. mikmaqi*; Hymenoptera: Apidae), *Melissodes bimaculatus* (Hymenoptera: Apidae) and small metallic green sweat bees (including *Augochlora pura*, *Augochlorella aurata*, and *Augochloropsis metallica*; Hymenoptera: Halictidae). Together, these morphospecies accounted for 65% of all visits to *C. sativus* (Table 3). Visitation by these three morphospecies showed divergent responses to urbanization, with *M. bimaculatus* visitation positively correlated, green sweat bee visitation negatively correlated, and *Ceratina* sp. visitation unrelated to urbanization (Table 4). NFD did not affect visitation by any of these morphospecies to *C. sativus* (Table 4).

Visitation to *H. annuus* was dominated by just two morphospecies: *Melissodes agilis* (Hymenoptera: Apidae) and *Halictus* sp. (Hymenoptera: Halictidae; includes *H. confusus*, *H. ligatus*, and *H. rubicundus*), which together accounted for 76% of all visits (Table 3). Visitation to *H. annuus* by both morphospecies declined with urbanization (Table 4). *Halictus* sp. visitation was marginally negatively affected by neighborhood total floral density, while *M. agilis* visitation was negatively affected by neighborhood Asteraceae floral density (Table 4). *M. agilis* visitation was significantly higher in garden plots (Table 4).

As a result of the patterns outlined above, the visitor community to both species changed significantly along the rural-to-urban gradient—though this explained only a small amount of the total variance in visitor community composition (*C. sativus*:  $R^2 = 0.06$ ,  $F = 6.67$ ,  $p < 0.001$ ; *H. annuus*:  $R^2 = 0.08$ ,  $F = 9.27$ ,  $p < 0.001$ ). In addition, visitor community composition was significantly affected by plot type for *H. annuus* ( $R^2 = 0.05$ ,  $F = 5.98$ ,  $p < 0.001$ ) but not for *C. sativus* ( $R^2 = 0.02$ ,  $F = 1.60$ ,  $p = 0.08$ ).

**Table 3** Bee morphospecies observed visiting *C. sativus* and *H. annuus*, with visitation frequency

Family	Morphospecies	<i>C. sativus</i>		<i>H. annuus</i>	
		# of visits	% of total	# of visits	% of total
Andrenidae	<i>Calliopsis andreniformis</i>	1	0.1	3	0.3
Apidae	<i>Apis mellifera</i>	39	3.8	24	2.0
	<i>Bombus fervidus</i>	1	0.1	0	0.0
	<i>Bombus impatiens</i>	83	8.1	38	3.2
	<i>Bombus</i> sp. 3	0	0.0	4	0.3
	<i>Ceratina</i> sp.	256	25.0	21	1.8
	Eucerini sp.	5	0.5	0	0.0
	<i>Melissodes agilis</i>	105	10.3	587	49.2
	<i>Melissodes bimaculatus</i>	242	23.7	34	2.9
Colletidae	<i>Hylaeus</i> sp.	5	0.5	3	0.3
Halictidae	<i>Agapostemon</i> sp.	16	1.6	32	2.7
	<i>Augochlora/Augochlorella</i>	161	15.7	23	1.9
	Halictid 1	0	0.0	1	0.1
	<i>Halictus</i> sp.	21	2.1	322	27.0
Megachilidae	<i>Lasioglossum</i> sp.	59	5.8	46	3.9
	<i>Anthidium</i> sp.	0	0.0	1	0.1
	<i>Megachile</i> large	0	0.0	14	1.2
	<i>Megachile</i> small	12	1.2	4	0.3
Unidentified bees		17	1.7	35	3.0
Total		1023		1192	

Morphospecies denoted with spp. includes multiple species in that genus that could not reliably be distinguished on the wing

**Table 4** Drivers of pollinator visitation by the most frequent pollinator morphospecies to *C. sativus* and *H. annuus*

Fixed Effect	<i>C. sativus</i>			<i>H. annuus</i>	
	<i>Ceratina</i> spp.	<i>Melissodes bimaculatus</i>	Green sweat bees	<i>Melissodes agilis</i>	<i>Halictus</i> spp.
	Estimate, <i>P</i>	Estimate, <i>P</i>	Estimate, <i>P</i>	Estimate, <i>P</i>	Estimate, <i>P</i>
Degree of urbanization	NA	<b>+ 2.20, &lt; 0.001</b>	<b>− 2.09, 0.002</b>	<b>− 1.41, 0.003</b>	− 1.40, 0.07
Neighborhood floral density	NA	NA	NA	NA	− 0.32, 0.16
Asteraceae neighborhood floral density	NA	NA	NA	<b>− 1.05, 0.02</b>	NA
Plot type (garden)	NA	NA	<b>+ 1.99, 0.03</b>	<b>+ 3.30, &lt; 0.001</b>	NA
Temperature	NA	NA	NA	+ 0.08, 0.77	− 0.16, 0.40
Year	+ 1.48, 0.07	NA	NA	<b>− 1.60, 0.002</b>	<b>+ 0.85, 0.02</b>

Boldface represents significant effects

## Discussion

This study reveals urbanization-mediated context dependence in floral neighborhood effect on pollinator visitation to *C. sativus* but not *H. annuus*. Urbanization had contrasting effects on pollinator visitation to the two species, weakly increasing visits to *C. sativus* while weakly decreasing visits to *H. annuus*. Similarly, increasing NFD reduced visitation to *H. annuus*, indicating competition for pollinators; by contrast, floral neighborhood had no effect on visitation to *C. sativus* when all plots were considered

together. However, separate consideration of urban and non-urban plots reveals contrasting effects of NFD on pollinator visitation to *C. sativus*: in non-urban plots, the effect of floral neighborhood was neutral, while in urban plots the effect was negative. Moreover, while *C. sativus* experienced facilitative effects of floral neighbors at low floral densities, this effect disappeared in urban plots. There was no such non-additive effect of urbanization and floral neighborhood in *H. annuus*, suggesting that in that species, the effect of pollinator-mediated plant–plant interactions are not contingent on urbanization context.



Context dependence in the effect of floral neighborhood on pollinator visitation to *C. sativus* may be the result of changes in (1) pollinator community composition, paired with species-specific foraging habits, and/or (2) pollinator foraging behavior along the urbanization gradient (Andrieu et al. 2009). Consistent with explanation 1, *C. sativus* floral visitor community composition did change significantly along the urbanization gradient. Yet while visitation by the most frequent visitors to *C. sativus* did show opposite responses to urbanization, there is no evidence for differences in these species' response to NFD, as would be expected if urbanization-driven changes in pollinator community composition were responsible for the context dependence. This raises the possibility that context dependence is the result instead of within-species shifts in foraging behavior along the rural-to-urban gradient, perhaps resulting from changes in floral community composition (e.g., increases in ornamental species in urban landscapes).

While these findings are consistent with my expectation that *C. sativus* would experience more context dependence in floral neighborhood effects on pollinator visitation, it appears that differences in pollinator community composition between *C. sativus* and *H. annuus*, rather than differences in floral attractiveness, account for the divergent outcomes for the two species. This highlights the need for improved understanding of how specific pollinators of interest, rather than the pollinator community in aggregate, respond to drivers of environmental change like urbanization, as well as to floral neighborhood.

Across both plant species, there was a strong positive effect of location within a community garden on pollinator visitation rates, even when controlling for total and con-familial floral density. This is most likely due to a greater availability of nesting sites within gardens. Nests of bumble bees (*Bombus* spp.), for example, occur at higher densities in gardens than other land-use types (Osborne et al. 2008a). Because bees are central-place foragers and tend to spend more time foraging close to their nest (Osborne et al. 2008b), the local aggregation of nests within a garden should lead to increased visitation to nearby plants. This finding highlights the importance of community gardens for maintaining pollination services in the wider landscape.

This study measured pollinator visitation rather than pollination; a change in visitation rate does not necessarily imply a meaningful change in pollination or plant reproductive success. Nevertheless, other researchers studying a range of both wild (Vázquez et al. 2005) and crop (Kleijn et al. 2015) plants have shown visitation rate to be a good proxy for pollination, despite interspecific differences in pollination effectiveness among flower visitors (but see King et al. 2013). Given that both plant species investigated here benefit from animal pollination, it is likely that

the observed changes in visitation with changes in urbanization and/or floral neighborhood affect reproductive success and yield. More direct measures of pollination and fertilization, such as per-visit transfer rates of conspecific pollen, would be preferable to visitation rate, but were difficult to obtain in this study.

I conclude that urbanization has the potential to alter interactions among co-flowering plants that share pollinators, though whether such an effect is widespread is unclear. The strength of this effect will depend on pollinators' response to urbanization and floral fidelity across floral contexts, traits that vary across pollinator taxa. Thus, the extent of context dependence in these interactions will likewise vary across plant species, but may be predictable if pollinator community composition is sufficiently well known.

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**Compliance with ethical standards**

**Conflict of interest** The authors declare that they have no conflict of interest.

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