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Pollination deficits increase with urbanization in Chicago

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Abstract

Urban growth is occurring rapidly, and the land use changes associated with urbanization may have consequences for pollinators and the plants that rely on them. Despite its importance in the face of pollinator declines and expanding urban ecosystems, our understanding of the effects of urbanization on pollination mutualisms is scant. There is both evidence that urban areas support diverse pollinator communities and evidence that they degrade them. The influence of urbanization on the pollination of urban plants is even less understood. Urban agriculture relies on plant–pollinator interactions for crop production, providing a relevant framework to study pollination in an urban context. We therefore grew 240 plants across six sites at varying levels of urbanization in Chicago, Illinois, to investigate how urbanization relates to pollination of *Cucurbita pepo* (squash) and the buzz-pollinated *Solanum lycopersicum* (tomato). We used a pollen limitation experiment to test whether the reproduction of plants at urban farms is pollen-limited and whether the magnitude of pollen limitation varies with the extent of urbanization (quantified as the percent of surrounding impervious surface around each site). We also examined how pollinator visitation rates vary with urbanization. In *S. lycopersicum* but not *C. pepo*, the pollen addition treatment had a consistent and significant positive effect on reproductive success, indicating that plants of *S. lycopersicum* are pollen-limited in our study area. The magnitude of pollen limitation increased with greater impervious surface, illustrating that *S. lycopersicum* plants at more urban sites are more pollen-limited. For *C. pepo*, there was only evidence of pollen limitation at the most urban site, and a weak trend of pollen limitation of fruit set (but not seed set) increasing with impervious surface. Our results demonstrate that urban plants are likely experiencing deficits in pollination services but in ways that vary with both the type of pollination system and the level of urbanization in the surrounding area.

KEYWORDS
bees, crop pollination, impervious surface, pollen limitation, pollinators, urban farms

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INTRODUCTION

Urbanization is occurring at an unprecedented rate and scale, and global urban expansion is predicted to increase almost threefold from 2000 to 2030 (Seto et al., 2010, 2012). Urban areas are characterized by impervious surface such as pavement, concrete, and other human-made structures that dominate the landscape, as opposed to pervious surfaces such as soil or vegetation. Broadly, urban environments appear to reduce species abundance and richness and homogenize the physical landscape and the biological communities that occupy them (McKinney, 2006, 2008; Piano et al., 2020). As a result, urbanization may pose a threat to pollinator communities and therefore the critical ecosystem services they provide.

Pollinators are threatened by a number of factors that may relate to or interact with urbanization, including habitat loss, climate change, invasive species, and pesticide use (Potts et al., 2010; Vanbergen & I. P. Initiative, 2013; Winfree et al., 2009). The increase in impervious surface, spatially disjointed development, and exacerbation of other threats associated with urbanization are hypothesized to have considerable consequences for pollinators and pollination services via destruction and fragmentation of suitable habitat, changes in plant community composition, and loss of nesting resources. However, these potential impacts of urbanization on pollination are understudied relative to other threats, and this has been highlighted as a critical research direction for pollination ecology (Knight et al., 2018). Urbanization has been repeatedly linked to lower pollinator abundance and less diverse pollinator communities (Ahrné et al., 2009; Burdine & McCluney, 2019; Geslin et al., 2016; Pereira et al., 2020), with one city in Brazil experiencing a 45% decline in bee species richness over 34 years of urban development (Cardoso & Gonçalves, 2018). These relationships, however, are highly variable across species, functional traits, and scales (Banaszak-Cibicka & Żmihorski, 2012; Bates et al., 2011; Cardoso & Gonçalves, 2018; Geslin et al., 2016).

The ways in which urbanization influences the pollination of urban plants are even less understood (Knight et al., 2018; Wenzel et al., 2020). Urbanization may impact plant–pollinator interactions by changing pollinator abundance, diversity, and behavior (Harrison & Winfree, 2015). Changes in the pollinator community may in turn reduce the quantity or quality of pollination services to plants, potentially jeopardizing plant reproduction. For example, pollen limitation occurs when seed or fruit production is limited by inadequate pollen receipt. While pollen limitation is commonly observed in natural populations (Burd, 1994; Knight et al., 2005), it appears to be a major driver of reproductive impairment for plants in fragmented habitats, such as those in urban environments (Aguilar et al., 2006). Loss of pollination may be especially pronounced for plants with more specialized floral morphology because their pollination is limited to a narrow subset of pollinators. If those pollinator species decline or are lost, there will be fewer alternative pollinators that can provide pollination services in their absence. For example, across several small conservation areas within an urban matrix in South Africa, the loss of a single bee species resulted in pollen limitation and seed set failure in six orchid species with a specialized pollination system, while a more generalist species was unaffected (Pauw, 2007).

Effects of urbanization on plant–pollinator interactions and pollen limitation can have implications for both wild and managed plant communities, such as in urban agriculture. Agriculture worldwide relies heavily on pollinators (Klein et al., 2007), and urban agriculture in particular is becoming increasingly important for urban growth, with almost one-fifth of global food production occurring in or near urban areas (Armar-Klemesu, 2000). Cities can support equal or even greater pollinator abundance and diversity than intensively used agricultural areas (Hall et al., 2017; Wenzel et al., 2020), making urban agriculture an important prospect in the face of growing food demand and concern over the preservation of plant and pollinator populations. Urban farms therefore provide a relevant and unique framework to study the impacts of urbanization on pollination services.

Here, we aimed to assess the effects of urbanization on pollination services across a series of urban farms within the City of Chicago, IL, USA. Specifically, we tested whether and how pollinator visitation and pollen limitation differ across varying levels of urbanization, as measured by impervious surface, in two different pollination systems. We focused on two plant species: *Solanum lycopersicum* (tomatoes; Solanaceae) and *Cucurbita pepo* (squash; Cucurbitaceae), two agriculturally important crops that each represent a unique pollination morphology and ecology. Our experiment took place within a network of urban farm sites across a gradient of urbanization, ranging from the urban core of Chicago, Illinois, USA, out into the suburbs, to investigate the following questions: (1) Is plant reproduction pollen-limited at urban farm sites? (2) How does urbanization affect the magnitude of pollen limitation? (3) How does urbanization affect pollinator visitation? We expected the magnitude of pollen limitation to increase with urbanization, and we expected this relationship to be stronger in *S. lycopersicum* because it requires buzz pollination to reproduce. We also hypothesized that pollinator visitation to these species would be negatively related to the

level of urbanization. Our work helps to fill an important gap in our understanding of how urbanization can impact pollination services to different plant species.

MATERIALS AND METHODS

Study species and sites

We conducted our experiment from June through October 2021, using two plant species: *S. lycopersicum* var. "Sungold" (Solanaceae), sun gold tomatoes, and *C. pepo* var. "Jaune et Verte" (Cucurbitaceae), patty pan squash. These species are both agriculturally important crops that are readily grown on urban farms in Chicago, and each represents a unique pollination morphology and ecology. *S. lycopersicum* flowers have poricidal anthers, a specialized floral morphology in which pollen is released only by bee species capable of sonication, or "buzz" pollination, such as *Bombus* (Apidae), *Xylocopa* (Apidae), and *Halictinae* (Halictidae) species (Buchmann, 1983). Cucurbits are monoecious and have staminate (male) and pistillate (female) flowers, the proportions of which will vary depending on how long a plant has been in flower, but overall, there are typically more staminate than pistillate flowers on a plant (Allesh et al., 2019; Ne Smith et al., 1994). *C. pepo* have a unique relationship with squash bees, *Peponapis* and *Xenoglossa* species (Apidae), where female bees collect pollen exclusively from cucurbit flowers (Hurd et al., 1971). These bees appear to be the most efficient pollinators of *Cucurbita* species; however, the flowers are still visited and pollinated by a variety of generalist pollinators, including the widespread European honeybee, *Apis mellifera* (Canto-Aguilar & Parra-Tabla, 2000; Kamo et al., 2022; McGrady et al., 2020; Serra & de Campos, 2010).

We worked with Windy City Harvest (WCH), an urban agriculture program through the Chicago Botanic Garden (CBG), to carry out our pollination experiment at five agricultural sites in Chicago, Illinois, and one site at the CBG in suburban Glencoe, Illinois, USA (six sites total). Study plants at urban sites were placed within WCH urban farms, surrounded primarily by other crop species growing in raised beds, and plants at the suburban site were in a botanical garden setting, surrounded largely by ornamental plants and species native to Illinois, including a fruit and vegetable garden. Following Gruver and CaraDonna (2021), we quantified urbanization as the percent of impervious land cover surrounding each site within a 500 m radius and 1000 m radius, calculated using ArcGIS 10.7.1 and 2019 impervious cover data from the USGS National Landcover Database (Multi-Resolution Land Characteristics Consortium, mrlc.gov). Impervious surface ranged from 49.3% to 71.5% at 500 m and 57.0% to 77.9% at 1000 m across the urban farm sites. Impervious surface was 19.7% at 500 m and 32.1% at 1000 m at the CBG (Table 1, Figure 1).

Pollen limitation experiment

We set up a pollination experiment to quantify pollen limitation and its magnitude in each species across our sites. Our experimental setup consisted of 120 plants of each of our two species, grown in a greenhouse from seed, then transplanted into grow bags at each study site (20 plants of each species at each of the six sites). We also had four pollen donor plants per species at each site in case we could not collect enough pollen from our experimental plants to cross with all open flowers. Seeds were planted at the WCH greenhouse for *S. lycopersicum* and the CBG greenhouse for *C. pepo* on 1 April 2021. Between 29 May and 2 June 2021, seedlings were transplanted into 26.5-L (7-gallon) fabric grow bags at each site using organic potting soil (Cowsmo Compost, Cochrane, WI). Plants were fertilized once per month and were scheduled to be watered three times per week; however, the growers at each site made decisions about increasing or decreasing watering based on local weather conditions.

For each species, we applied a pollen addition treatment to 10 individuals at each site, while the other 10 served as unmanipulated, open-pollinated controls (i.e., ambient pollination). Plants were placed in two to four rows, depending on the space available at each site, and arranged in a paired design, with each pair consisting of one control and one supplemental plant

TABLE 1 The percent of impervious surface at 500 and 1000 m radii surrounding study sites at the Chicago Botanic Garden (CBG) and Windy City Harvest farms in Chicago.

Site	Impervious surface (%)		Farm size (ha)
	500 m	1000 m	
Chicago Botanic Garden	19.7	32.1	...
Washington Park Youth Farm	49.3	57.0	0.30
PCC Austin	66.7	67.0	0.10
Farm on Ogden	72.2	72.4	0.10
Legends	76.1	74.3	0.81
Kenneth	77.2	77.9	0.10

Note. Farm size is not applicable at the CBG as this site is not a farm and lacks distinct boundaries within an urban matrix.

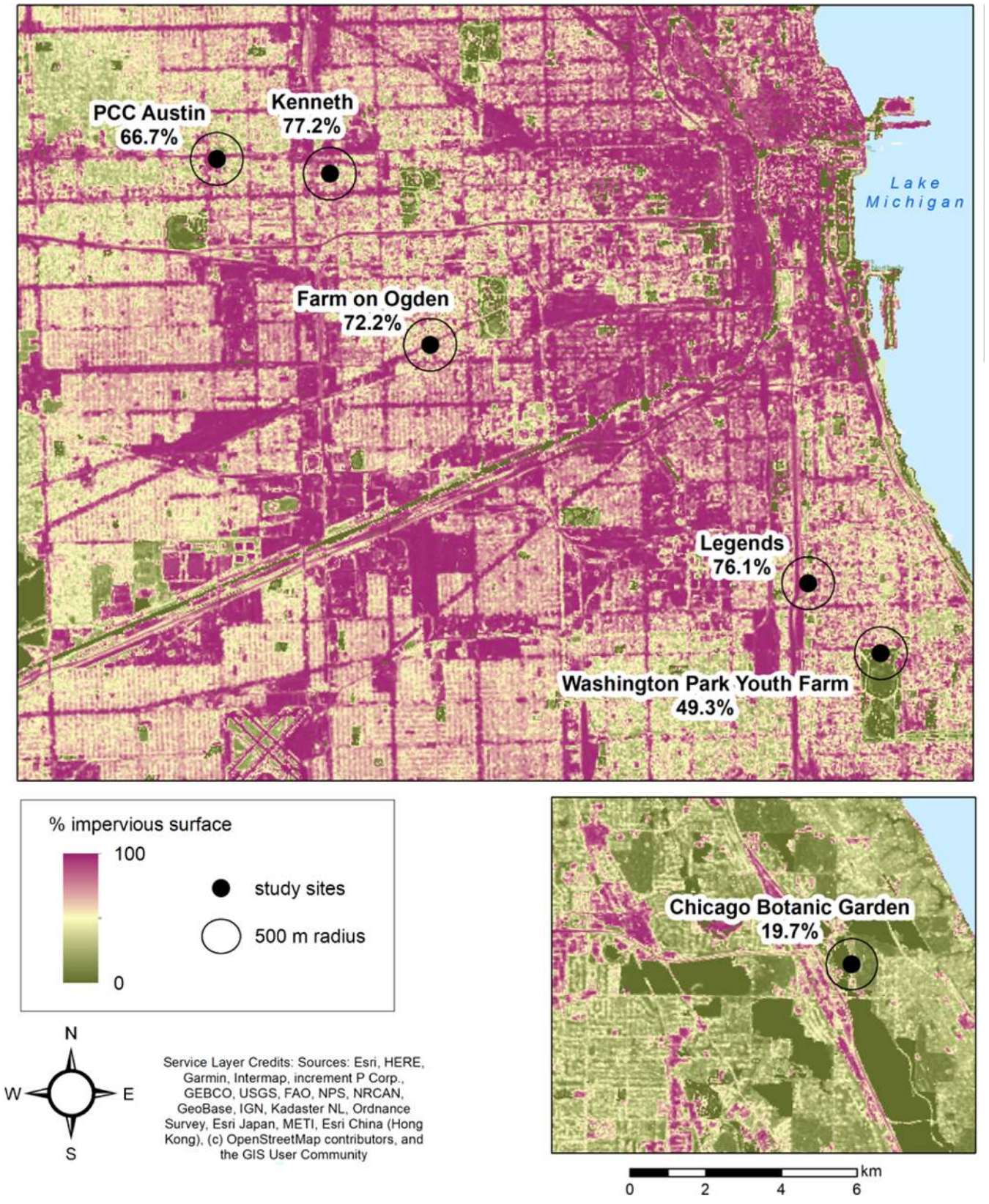

FIGURE 1 Map of study area showing six study sites and percent of surrounding impervious cover. Circles represent the 500-m radii around each site that was used to determine surrounding impervious surface.

placed side by side, 30 cm apart, to account for potential fine-scale variation within each site (e.g., shade; Appendix S1: Figure S1). The plants were all approximately the same size in terms of aboveground biomass at the time of setup because they were all grown from seed at the same time. Therefore, plants were paired haphazardly and pollination treatment was randomly assigned within each pair. We applied supplemental outcross pollen to the stigmas of all open flowers on pollen-supplemented plants twice weekly, weather permitting, as hand pollination was not possible during rain. We pollinated *C. pepo* flowers by collecting pollen from the anthers of open male flowers with a paintbrush and transferring it directly to the stigma of open female flowers on a different plant. We pollinated *S. lycopersicum* flowers using VegiBee Garden Pollinators (VegiBee, China), vibrating tools that mimic insect sonication. We sonicated each open flower on a supplemental plant, collecting the pollen in a spoon and using it to pollinate all open flowers on another experimental plant by dipping the stigmas into the pollen. At each visit, we counted all open flowers on control and supplemental plants. On supplemental plants, if there were any flowers that had opened and closed since our last visit, causing us to miss the window of opportunity for pollination, we marked these flowers using twist-ties and did not include them in our assessment of pollen limitation.

We harvested fruits twice weekly, counting and harvesting all fruits that were at the stage that local farmers consider ready to harvest. For *S. lycopersicum*, this is when the fruits reach a deep orange color and readily come off the vine when tugged gently. For *C. pepo*, this is when the fruits are between 5 and 10 cm in diameter. Half of the fruits harvested from each individual plant were transported to and frozen at the CBG for measures of reproductive success. If an individual produced more than 10 fruits in 1 week, a subset of five fruits were used, due to the logistics of collecting and then processing that number of fruits. We considered both ecologically and agriculturally relevant measures of reproductive success: the proportion of flowers that set fruit, number of seeds produced per fruit, mass of fruit, and size of fruit. We measured fruit size using diameter in the longest direction between the stem end and blossom end. We did not consider size or mass measures for *C. pepo* because fruits continue to grow larger the longer they stay on the plant, far beyond the optimal size for harvesting, so size and mass reflect when the fruits were harvested. We measured the magnitude of pollen limitation as the difference in reproductive success between control and pollen-supplemented plants for each measure of reproductive success.

Pollinator visitation

We quantified the rate of pollinator visitation to each of our focal species using a combination of in-person observations and video. To include the entire range of potential visitors to our flowers, observations were conducted between 0900 and 1800 h during non-rainy weather. For each observation period, we selected a group of flowers from one to three plants for which we could observe each flower simultaneously. For *S. lycopersicum*, this ranged from 4 to 88 flowers per observation session, and for *C. pepo*, one to five flowers. For video observations, GoPro Hero or Hero4 cameras (GoPro, San Mateo, CA) were stationed 15–45 cm in front of open flowers and recorded videos that were later scored for visits. Human observations were conducted in 10-min observation sessions. Video observations ranged in length from 25 to 55 min, depending on the camera used. We conducted three to six observation sessions weekly for each species when flowers were open for a total of 405–869 min per species per site across the growing season, for a total of 4170 min for *S. lycopersicum* and 3708 min for *C. pepo*. Because human observations and video recordings observed different numbers of flowers for different lengths of time, we standardized our observations to a visitation rate. We calculated visitation rates for each observation period as the number of visits per flower per minute. For *S. lycopersicum*, we considered a visit to be any instance where a floral visitor landed and remained on the anther cone of a flower for more than 1 s, in order to exclude visitors that were not actually sonicating the flowers. For *C. pepo*, we considered a visit to be any instance where a floral visitor came in contact with the anthers or stigma of a flower. We identified visitors to the lowest taxonomic level possible in the field or from video resolution, often to the species level for bumblebees (*Bombus* spp.), European honeybees (*A. mellifera*), and squash bees (*Peponapis pruinosa*).

Statistical analysis

If pollen-supplemented plants have greater reproductive success than control plants within our experimental pairs, this indicates that plant reproduction is pollen-limited. We first tested for pollen limitation within each site using linear mixed-effects models (LMMs) and generalized linear mixed-effects models (GLMMs) using the lme4 (Bates et al., 2015) and glmmTMB (Brooks et al., 2017) packages respectively with treatment (pollen addition vs. control) as a predictor, measures of reproductive success as response

variables (fruit to flower ratio, seeds per fruit, fruit size, and fruit mass), and experimental pair as a random intercept term. Plant individual was also included as a random intercept term for responses that were measured multiple times within individuals (seeds per fruit, fruit size, and fruit mass). We used GLMMs for fruit and seed set, with a binomial error distribution for fruit set, or betabinomial when overdispersed, and a Poisson distribution for seed set, or negative binomial when overdispersed. We used LMMs for fruit size and mass. Because individuals produced varying numbers of flowers, fruit set models were weighted by the number of flowers produced by each individual. We used a Bonferroni correction to determine our critical p value for significance to account for multiple tests. As we repeated each test for each of our six sites, our critical p value is 0.0083 (0.05/6).

Second, to investigate the relationship between impervious surface and the magnitude of pollen limitation, we used linear models with impervious surface as our predictor variable, and the differences in reproductive success within pairs as response variables. To calculate the difference, control reproductive responses were subtracted from supplement responses for each plant pair within each site. Because impervious surface at 500 and 1000 m radii were highly correlated ($r = 0.99$, $p < 0.001$) and produced consistent results, we focus only on impervious surface at 500 m for our analyses. We also performed the same analysis with open pollination efficiency as the response variable (open reproduction/supplemental reproduction; Ne'eman et al., 2010), to ensure that the metric of pollen limitation did not influence the results.

To assess how impervious surface related to pollinator visitation, we used GLMMs with impervious surface as a predictor variable, visitation rate per flower per minute as a response variable, and date as a random intercept to account for repeated sampling of pollinator visitation across multiple days. Because our visitation rates were based on observations conducted across varying numbers of flowers, we also weighted our model by the number of flowers observed. We used a betabinomial error distribution because our visitation data were overdispersed. For one observation period in *C. pepo*, the visitation rate was slightly greater than 1 (1.044); we rounded this value to 1 to fit the betabinomial model. To determine whether visitation patterns were driven by the most frequently observed pollinators or by the taxa expected to be the most effective, we also ran the visitation rate models with only *Bombus* spp. and only "other bees," those too small to identify in the field, for tomato and with only *P. pruinosa* for squash (which was the most frequent and expected visitor).

RESULTS

Over 13 weeks, we observed 116 pollinators across at least three genera visiting *S. lycopersicum* and 330 pollinators across at least five genera visiting *C. pepo* flowers. Of the visitors to *S. lycopersicum*, bees we could not identify to genus made up 55.7% of visits, followed by *Bombus* (40.2%), *Agapostemon* (2.4%), and *A. mellifera* (1.7%). *Bombus* spp. were observed visiting *S. lycopersicum* flowers at each site, whereas *A. mellifera* and *Agapostemon* were only observed at one site each (Appendix S1: Figure S2). Squash bees (*P. pruinosa*) made up 54.8% of visits to *C. pepo*, followed by insects we could not identify to genus (18.1%), European honeybees (*A. mellifera*) (13.3%), and bees in the genera *Melissodes* (9.8%), *Bombus* (2.9%), and *Agapostemon* (1.1%). *P. pruinosa* were observed visiting *C. pepo* flowers at each site except the most urban site (Appendix S1: Figure S2). The average visitation rate, across all sites and observation sessions, to *S. lycopersicum* was 0.010 visits per flower per minute, and the average visitation rate to *C. pepo* was almost four times higher, at 0.039 visits per flower per minute.

On average, *S. lycopersicum* control plants matured 83.6% ± 1.4% (±1 SE) of their flowers into fruits, and pollen-supplemented plants matured 93.6% ± 0.9% of their flowers into fruits. *S. lycopersicum* control plants on average produced 41.4 ± 0.68 seeds per fruit compared to 53.6 ± 0.51 seeds per fruit in pollen-supplemented plants. On average, *C. pepo* plants matured a lower proportion of their flowers into fruits; control plants matured 43.4% ± 3.9% of their flowers into fruits, and pollen-supplemented plants matured 59.6% ± 3.8% of their flowers into fruits. *C. pepo* control plants on average produced 181.2 ± 4.6 seeds per fruit compared to 202.3 ± 5.5 seeds per fruit in pollen-supplemented plants.

Pollen limitation in *S. lycopersicum* increased with impervious surface across all measures of reproduction: fruits per flower ($R^2 = 0.23$, $F_{1,58} = 18.99$, $p < 0.0001$), seeds per fruit ($R^2 = 0.43$, $F_{1,58} = 46.29$, $p < 0.0001$), fruit mass ($R^2 = 0.24$, $F_{1,58} = 19.28$, $p < 0.0001$), and fruit diameter ($R^2 = 0.28$, $F_{1,58} = 23.91$, $p < 0.0001$; Table 2, Figures 2 and 3). All four reproductive measures were significantly pollen-limited across all sites, except for fruit mass and diameter at our suburban site with the least surrounding impervious surface (19.7%, CBG; Table 3, Figures 2 and 3).

Across sites, the magnitude of pollen limitation in *C. pepo* increased marginally with impervious surface for fruit set ($R^2 = 0.04$, $F_{1,58} = 3.68$, $p = 0.060$), but there was no effect for seed set ($R^2 = -0.04$, $F_{1,26} = 0.0017$, $p = 0.97$; Table 2, Figure 4a). Note that R^2 values from a linear model can be negative (Chicco et al., 2021). *C. pepo* fruit set was not significantly pollen-limited at any of the

TABLE 2 Responses of the magnitude of pollen limitation (in terms of difference in reproduction) between paired control and supplemental plants, with percent impervious surface as a predictor.

Species	Response	Slope estimate ± 1 SE	*t*	*p*
Solanum lycopersicum	Difference in fruit set	0.0021 ± 0.0005	4.36	<0.0001
	Difference in seed set	0.16 ± 0.02	6.80	<0.0001
	Difference in mass	0.0098 ± 0.002	4.39	<0.0001
	Difference in diameter	0.0021 ± 0.0004	4.89	<0.0001
Cucurbita pepo	Difference in fruit set	0.0048 ± 0.002	1.92	0.0601
	Difference in seed set	−0.016 ± 0.39	−0.042	0.967

six sites. Seed set was significantly pollen-limited at one of the six sites, the site with the highest level of impervious surface (77.2%, Kenneth) (Table 3, Figure 4b).

Results for open pollination efficiency mirrored those for pollen limitation. Open pollination efficiency in *S. lycopersicum* decreased with impervious surface across all measures of reproduction: fruits per flower ($R^2 = 0.23$, $F_{1,58} = 19.08$, $p < 0.0001$), seeds per fruit ($R^2 = 0.49$, $F_{1,58} = 58.68$, $p < 0.0001$), fruit mass ($R^2 = 0.31$, $F_{1,58} = 27.28$, $p < 0.0001$), and fruit diameter ($R^2 = 0.30$, $F_{1,58} = 26.69$, $p < 0.0001$; Table 4). Open pollination efficiency in *C. pepo* also decreased with impervious surface for fruit set ($R^2 = 0.077$, $F_{1,54} = 5.57$, $p = 0.021$) but not for seed set ($R^2 = -0.04$, $F_{1,26} = 0.013$, $p = 0.91$; Table 4).

Pollinator visitation varied with impervious surface for some species, but in general, impervious surface did not explain more than 15% of variation in pollinator visitation rates. For *S. lycopersicum*, the rate of pollinator visitation decreased with greater surrounding impervious surface ($R^2{}_m = 0.073$, $p = 0.015$, estimate ± SE = −0.023 ± 0.01; Figure 5a), consistent with increasing pollen limitation with impervious surface. The rate of visitation by *Bombus* spp. did not relate to impervious surface ($R^2{}_m = 0.052$, $p = 0.174$, estimate ± SE = −0.019 ± 0.01; Figure 5c), while visitation by small bees decreased marginally with impervious surface ($R^2{}_m = 0.089$, $p = 0.063$, estimate ± SE = −0.026 ± 0.01; Figure 5e). In contrast, the rate of visitation for *C. pepo* did not change significantly with impervious surface ($R^2{}_m = 0.007$, $p = 0.56$, estimate ± SE = 0.007 ± 0.013; Figure 5b). The rate of visitation by *P. pruinosa* increased marginally with impervious surface ($R^2{}_m = 0.148$, $p = 0.093$, estimate ± SE = 0.049 ± 0.03; Figure 5d).

DISCUSSION

Urbanization is a prominent form of land use change, but we do not have a clear picture of how urban development influences interspecific interactions, including those that occur among plants and pollinators. This understanding is important not only for wild plant and pollinator populations but also for the pollination services that generate food production for humans (Klein et al., 2007; Ollerton, 2017). Across a network of urban farms spanning a gradient of urbanization in the city of Chicago, we found that pollen limitation increases with increasing urbanization for one of our two study species. In *S. lycopersicum* (tomato), we found that both ecologically and agriculturally important measures of pollination success were consistently limited by pollination services. Critically, we observed pollen limitation across all sites, but the magnitude of pollen limitation was greater at more urban sites (i.e., those with greater surrounding impervious surface). In contrast, for *C. pepo* (squash), we found little evidence of pollen limitation, although seed set was pollen-limited at our most urban site. Consistent with our general prediction, impervious surface increased the magnitude of pollen limitation of fruit set, but for *C. pepo*, this was a weak effect and one that we did not find for seed set. Taken together, our results suggest that the increase in impervious surface associated with urbanization can have negative consequences for the pollination and reproduction of plants.

We tested for pollen limitation across an urbanization gradient in two species with different pollination ecologies. *S. lycopersicum* relies on bees with a specialized foraging behavior (buzz pollination) and exhibited nearly ubiquitous pollen limitation that was greater in magnitude at sites in more heavily urbanized areas. *C. pepo*, which can be pollinated by most bees and other insect pollinators, displayed little evidence of pollen limitation (only at the most urban site). These findings are consistent with broad trends across species of how pollen limitation responds to land use change, where plants in urban habitats tend to be more pollen-limited than those in natural or managed landscapes (Bennett et al., 2020). However, studies that investigated the effects of urbanization at the species level have focused on reproduction in wild plant species and thus far reported mixed results. Species have exhibited no change in reproduction between urban and rural sites (Barker & Sargent, 2020; Verboven et al., 2012), greater pollen limitation in urban sites (Carper et al., 2022; Hou et al., 2019), or less pollen limitation in urban sites (although this was in an invasive species; Parker, 1997). There is evidence that plants with more specialized pollination may be especially vulnerable

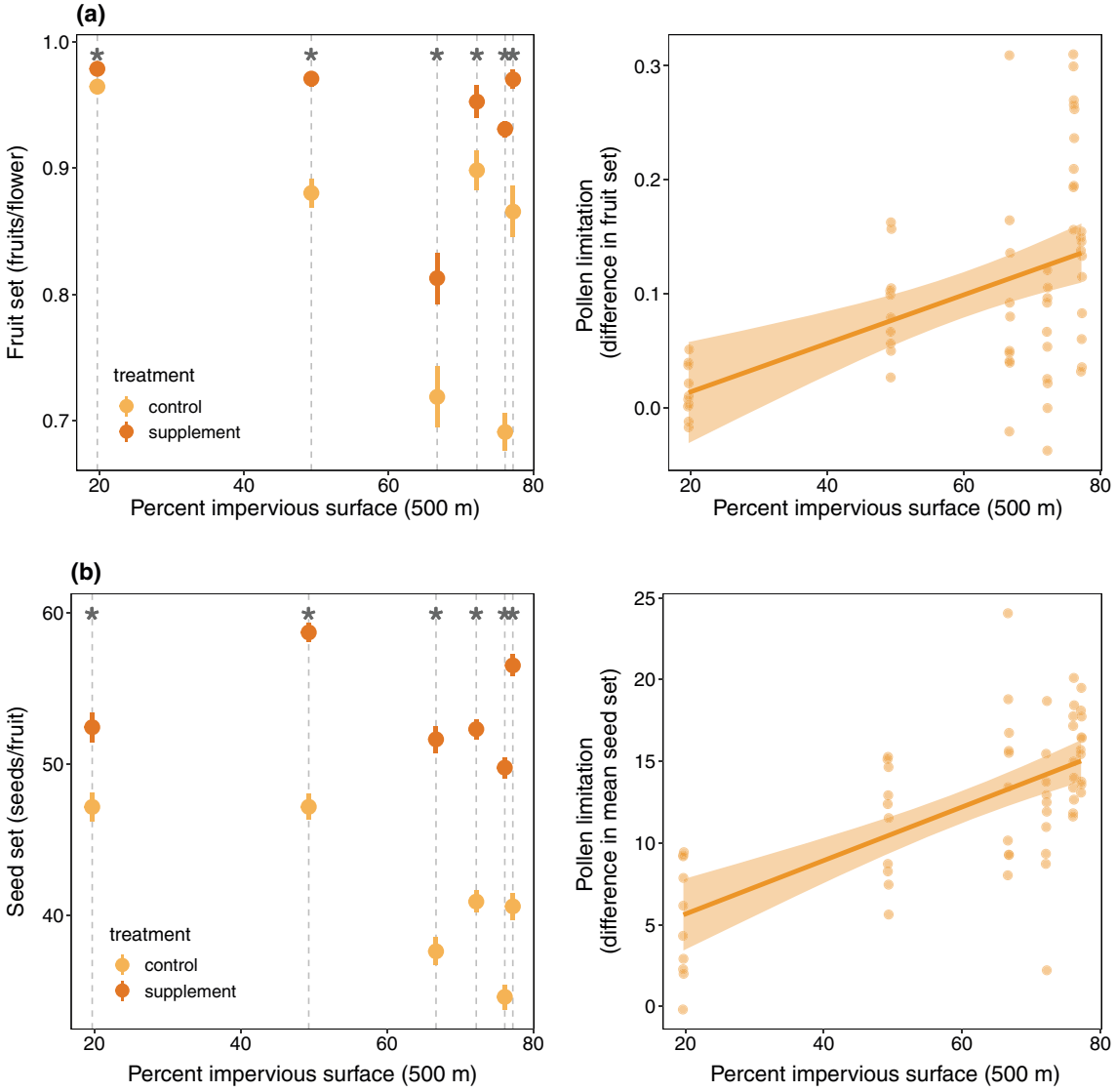

FIGURE 2 *Solanum lycopersicum* (tomato) (a) fruit set and pollen limitation of fruit set and (b) seed set and pollen limitation of seed set. Asterisks denote sites with significant treatment effects based on generalized linear mixed-effects models. Dots and error bars in left-hand panels are site-level means and SE. Vertical dashed lines are a visual tool to help compare between treatments within each site. Each dot in right-hand panels is the difference in reproduction between control and supplemental individuals within each experimental pair (supplement–control). Error around line of fit is SE.

to pollen limitation (Bennett et al., 2020). Although *S. lycopersicum* requires buzz pollination, a diversity of solitary bee and bumble bee species was observed performing this behavior, suggesting that there were not necessarily fewer species of effective pollinators compared to *C. pepo*. Urbanization likely has varying effects between species and study systems, and the pattern of specialized species being more pollen-limited has only been observed when broadly comparing urban to nonurban plants between different sites (Bennett et al., 2020), as opposed to the same species in urban versus nonurban sites or across an urbanization gradient. Research incorporating multiple specialized and generalized species within the same system is needed to understand whether and how specialization level affects pollen limitation of plant reproduction, and therefore which species may be more susceptible in urban environments.

In the context of urban ecosystems, patterns in pollination services should be assessed across a gradient of urbanization rather than placing sites into discrete urban or nonurban categories. For example, even within our heavily urbanized sites (impervious surface > 60%), we observed substantial variation in pollen limitation and visitation, suggesting that responses to urbanization are complex and may depend not only on whether a habitat

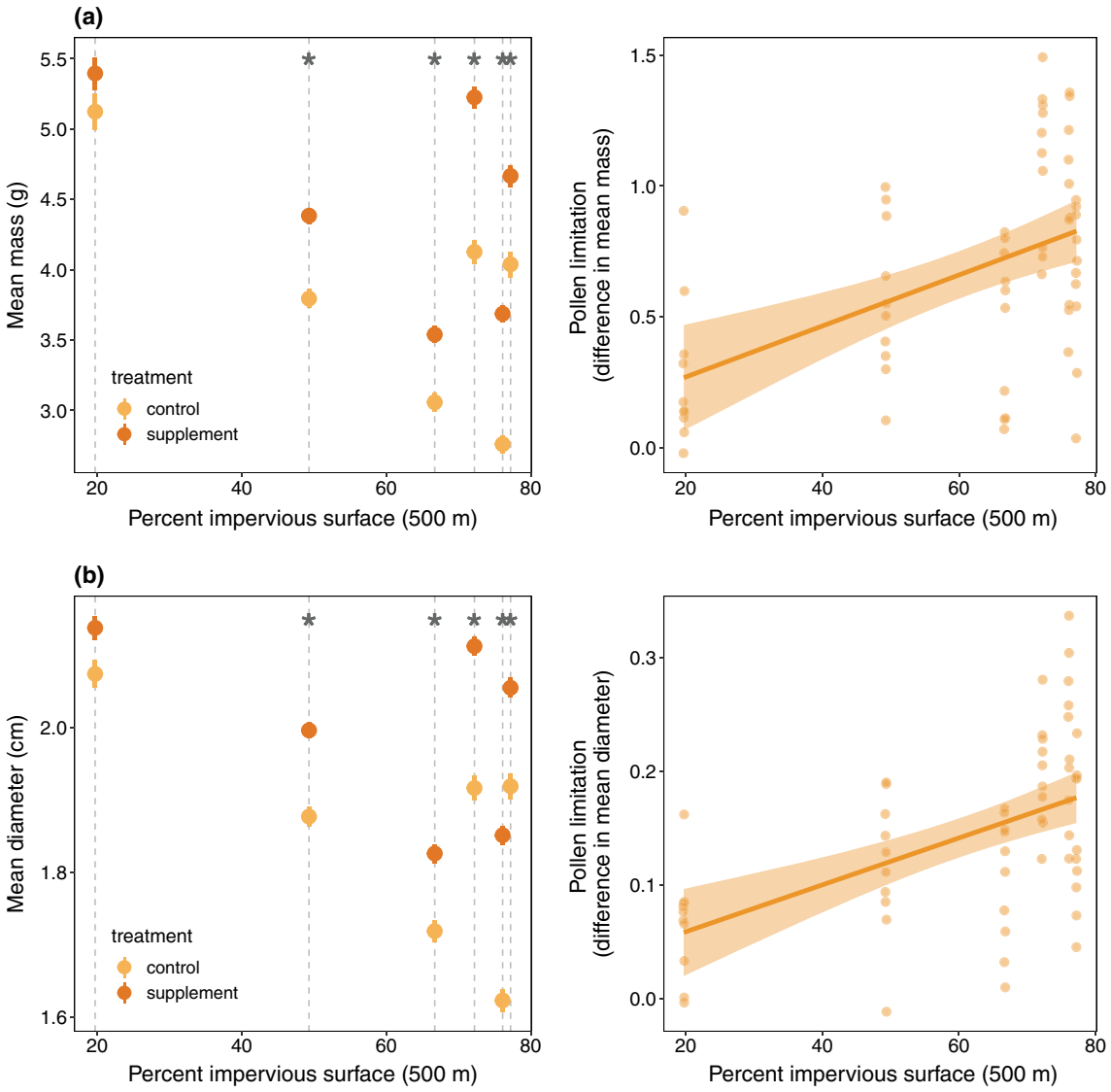

FIGURE 3 *Solanum lycopersicum* (tomato) (a) fruit mass and pollen limitation of mass and (b) fruit diameter and pollen limitation of diameter. Asterisks denote sites with significant treatment effects based on linear mixed-effects models. Dots and error bars in left-hand panels are site-level means and SE. Vertical dashed lines are a visual tool to help compare between treatments within each site. Each dot in right-hand panels is the difference in reproduction between control and supplemental individuals within each experimental pair (supplement–control). Error around line of fit is SE.

is considered urban, but the degree of urbanization as well as other factors beyond impervious surface. Our study in the Chicago area contained six sites across a gradient of urbanization, ranging from ~20% to 80% impervious surface, but only two sites had less than 50% impervious surface; a more ideal setup would have included more sites spaced more evenly across such a gradient. Local habitat characteristics such as the amount of available green space, gardening practices used in surrounding areas, nest site availability, and floral and nesting resources from home gardens and other plantings are likely to vary considerably across the urban landscape and could play an important role in shaping pollinator communities. Additionally, environmental factors such as heat, light, and soil moisture can affect tomato reproduction by limiting pollen production, pollen viability, and fruit production (Dingley et al., 2022), and the sex ratio of *C. pepo* flowers at the population or landscape scale might also influence reproduction (Allesh et al., 2019). However, our study plants were paired to control for any within-site environmental variation and randomly assigned to a treatment, so there should not be any strong bias in our results due to the abiotic environment or flower sex ratios. Furthermore, because we were working within a set of established and functioning urban farms in different areas of Chicago, we could not

TABLE 3 Responses of reproductive success measures to treatment (pollen supplementation) within each site.

Species	Site	Impervious surface (%)	Response	Test statistic	*p*	Mean difference
Solanum lycopersicum	CBG	19.7	Fruit set	3.0	0.0024	0.01
	WPF	49.3		8.8	<0.001***	0.09
	PCC	66.7		3.4	<0.001***	0.09
	FOO	72.2		5.7	<0.001***	0.05
	LEG	76.1		14.5	<0.001***	0.24
	KEN	77.1		10.2	<0.001***	0.10
	CBG	19.7	Seed set	3.8	<0.001***	5.32
	WPF	49.3		10.5	<0.001***	11.19
	PCC	66.7		9.7	<0.001***	14.09
	FOO	72.2		10.1	<0.001***	11.65
	LEG	76.1		12.8	<0.001***	15.19
	KEN	77.1		14.1	<0.001***	15.98
	CBG	19.7	Mass	2.4	0.15	0.28
	WPF	49.3		43.3	<0.001***	0.57
	PCC	66.7		21.2	<0.001***	0.46
	FOO	72.2		96.3	<0.001***	1.10
	LEG	76.1		75.3	<0.001***	0.92
	KEN	77.1		20.7	<0.001***	0.64
	CBG	19.7	Size	6.4	0.034	0.07
	WPF	49.3		38.9	<0.001***	0.12
	PCC	66.7		23.4	<0.001***	0.10
	FOO	72.2		87.7	<0.001***	0.20
	LEG	76.1		92.3	<0.001***	0.23
	KEN	77.1		28.8	<0.001***	0.14
Cucurbita pepo	CBG	19.7	Fruit set	1.1	0.25	0.04
	WPF	49.3		0.3	0.80	−0.04
	PCC	66.7		1.8	0.07	0.21
	FOO	72.2		1.6	0.12	0.20
	LEG	76.1		1.4	0.16	0.23
	KEN	77.1		1.9	0.05	0.33
	CBG	19.7	Seed set	2.4	0.02	24.96
	WPF	49.3		−0.3	0.75	−82.00
	PCC	66.7		0.6	0.53	15.53
	FOO	72.2		0.4	0.69	11.60
	LEG	76.1		1.6	0.11	22.92
	KEN	77.1		3.6	<0.001***	59.50

Note: For generalized linear mixed-effects models (fruit set and seed set), the test statistic is the *z* value. For linear mixed-effects models (mass and size), the test statistic is the *F* statistic. After Bonferroni correction, our critical *p* value is 0.0083. Mean difference in each reproductive success response between control and supplemental plants within each pair represents the magnitude of pollen limitation.

Abbreviations: CBG, Chicago Botanic Garden; FOO, Farm on Ogden; KEN, Kenneth; LEG, Legends; PCC, PCC Austin; WPF, Washington Park Youth Farm.

***Significant effects of treatment at $p < 0.001$.

control for small-scale variation in conditions such as heat and sunlight, or neighborhood influences like the surrounding floral landscape and nearby pesticide use. Studies that have examined pollinator communities across urbanization gradients have identified local habitat factors that may interact with or offset effects of

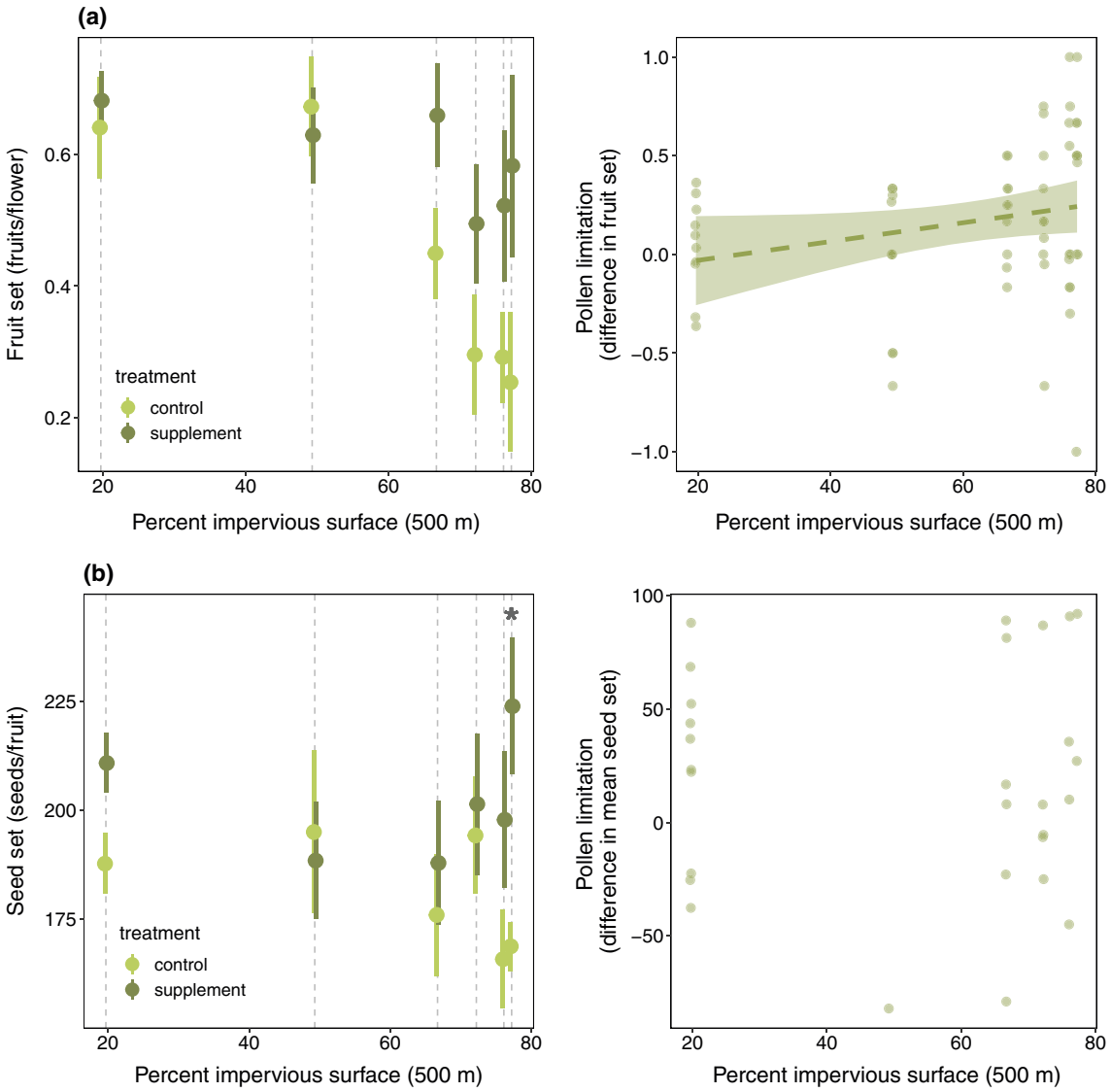

FIGURE 4 *Cucurbita pepo* (squash) (a) fruit set and pollen limitation of fruit set and (b) seed set and pollen limitation of seed set. Asterisk denotes one site with a significant treatment effect based on generalized linear mixed-effects models. Dots and error bars in left-hand panels are site-level means and SE. Vertical dashed lines are a visual tool to help compare between treatments within each site. Each dot in right-hand panels is the difference in reproduction between control and supplemental individuals within each experimental pair. The dashed line represents a marginally significant relationship ($0.05 < p < 0.10$). Error around line of fit is SE.

landscape-level urbanization alone, such as floral resources, pollinator foraging regime, habitat patch size, and season (Birdshire et al., 2020; Choate et al., 2018; Gruver & CaraDonna, 2021; Rivkin et al., 2020; Williams & Winfree, 2013). Indeed, in both species, reproductive success was variable across sites in the supplemental pollination treatment where plants should be receiving sufficient pollen and was particularly low at a site with an intermediate level of impervious surface (66.7%), providing evidence that other factors we did not examine affected reproduction. Our results highlight the need for more studies addressing the impacts of urbanization along urbanization gradients rather than landscape categories, and incorporating local habitat characteristics, to tease apart the relationships among urbanization, pollination services, and plant reproduction, as well as the mechanisms driving them (Wenzel et al., 2020).

If crops are pollen-limited in response to urbanization as we have shown for *S. lycopersicum*, then urban farms, especially those in heavily urbanized areas, are likely underproducing. Understanding the drivers of pollination services and pollen limitation in urban areas is necessary to improve crop production at urban farms and support the reproduction of wild and managed plant populations in or near urban habitats. Pollinator visitation rates to *S. lycopersicum* flowers decreased with

TABLE 4 Responses of open pollination efficiency (OPE), control reproduction/supplemental reproduction for each plant pair, to variation in percent impervious surface.

Species	Response	Predictor	Slope ± 1 SE	*t*	*p*
Solanum lycospersicum	OPE fruit set	Intercept	1.03 ± 0.034	30.72	<0.0001
		Impervious surface	−0.0023 ± 0.0005	−4.37	<0.0001
	OPE seed set	Intercept	0.96 ± 0.026	36.47	<0.0001
		Impervious surface	−0.0032 ± 0.0004	−7.66	<0.0001
	OPE mass	Intercept	1.00 ± 0.030	33.42	<0.0001
		Impervious surface	−0.0025 ± 0.0005	−5.22	<0.0001
	OPE diameter	Intercept	0.99 ± 0.013	73.74	<0.0001
		Impervious surface	−0.0011 ± 0.0002	−5.17	<0.0001
Cucurbita pepo	OPE fruit set	Intercept	0.84 ± 0.14	6.22	<0.0001
		Impervious surface	−0.0051 ± 0.0022	−2.36	0.022
	OPE seed set	Intercept	0.93 ± 0.12	7.76	<0.0001
		Impervious surface	0.0002 ± 0.0021	0.11	0.91

Note: Results are from linear models. One was added to squash fruit set and then log transformed to meet model assumptions.

impervious surface, suggesting that reduced visitation rates are part of the explanation for the increase in pollen limitation at more urban sites. We emphasize "part of" the explanation because impervious surface did not explain much variation in visitation rate. Pollen limitation is a consequence of insufficient pollen receipt, which could be the result of a deficit in either the quantity or quality of pollen received. Pollen limitation could increase with urbanization as a result of low pollinator visitation, as decreases in pollinator abundance and richness have been observed in response to urbanization across a range of systems and taxa (Ahrné et al., 2009; Cardoso & Gonçalves, 2018; Choate et al., 2018; Fortel et al., 2014; Geslin et al., 2013; Pereira et al., 2020). These declines are likely due to a combination of factors such as habitat fragmentation and loss of floral or nesting resources and could substantially reduce visitation to plants in these areas. Declining pollinator populations in response to urbanization might explain the contrasting patterns we found between our focal species. The lower visitation rates and greater pollen limitation seen in *S. lycopersicum*, which relies on bees capable of sonication, may reflect a reduced abundance of these pollinators. *C. pepo*, which can be pollinated by many bees as well as other insect pollinators, may have a greater buffer against declining pollinator populations as it can use a much broader range of visitors.

On the other hand, the pollen limitation and visitation patterns we observed may be related to more nuanced changes in plant–pollinator interactions rather than overall pollinator abundance. Specifically, changes in pollinator community composition or foraging behavior could also be limiting plant reproduction by decreasing the quality of pollination services provided to plants. There is support for the idea that urban and suburban areas can serve as refuges to pollinators, with neutral or even positive impacts of urbanization on pollinator groups like bees (Carper et al., 2014; Hall et al., 2017; Theodorou et al., 2017), especially when compared to primarily agricultural landscapes (Wenzel et al., 2020). In Chicago specifically, studies have found diverse wild bee communities that support pollination services to plants, where bee richness was most related to floral diversity rather than impervious surface (Gruver & CaraDonna, 2021; Lowenstein et al., 2015). However, the pollinator community differed in that highly urban areas housed more non-native bee species and fewer native species than less urban areas (Gruver & CaraDonna, 2020, 2021).

The increase in pollen limitation and lower visitation rates that we observed in *S. lycopersicum* in response to urbanization may therefore reflect shifts in pollinator community composition. Pollination of *S. lycopersicum* was carried out primarily by solitary bees we could not identify in the field, followed by bumblebees (*Bombus* spp.). *Bombus* visitation was not related to impervious surface, suggesting that their abundance or pollination behavior is not strongly driving pollen limitation, despite being one of the most studied and commonly used group of pollinators for supplemental pollination in *S. lycopersicum* (Cooley & Vallejo-Marín, 2021). Visitation by other, smaller bees decreased marginally with urbanization. The decreased pollinator visitation and greater pollen limitation we found in *S. lycopersicum* at more urban sites are therefore likely driven by these other bee species. Although their buzz pollination behavior and efficiency is less studied, smaller and often solitary bees such as *Lasioglossum* and

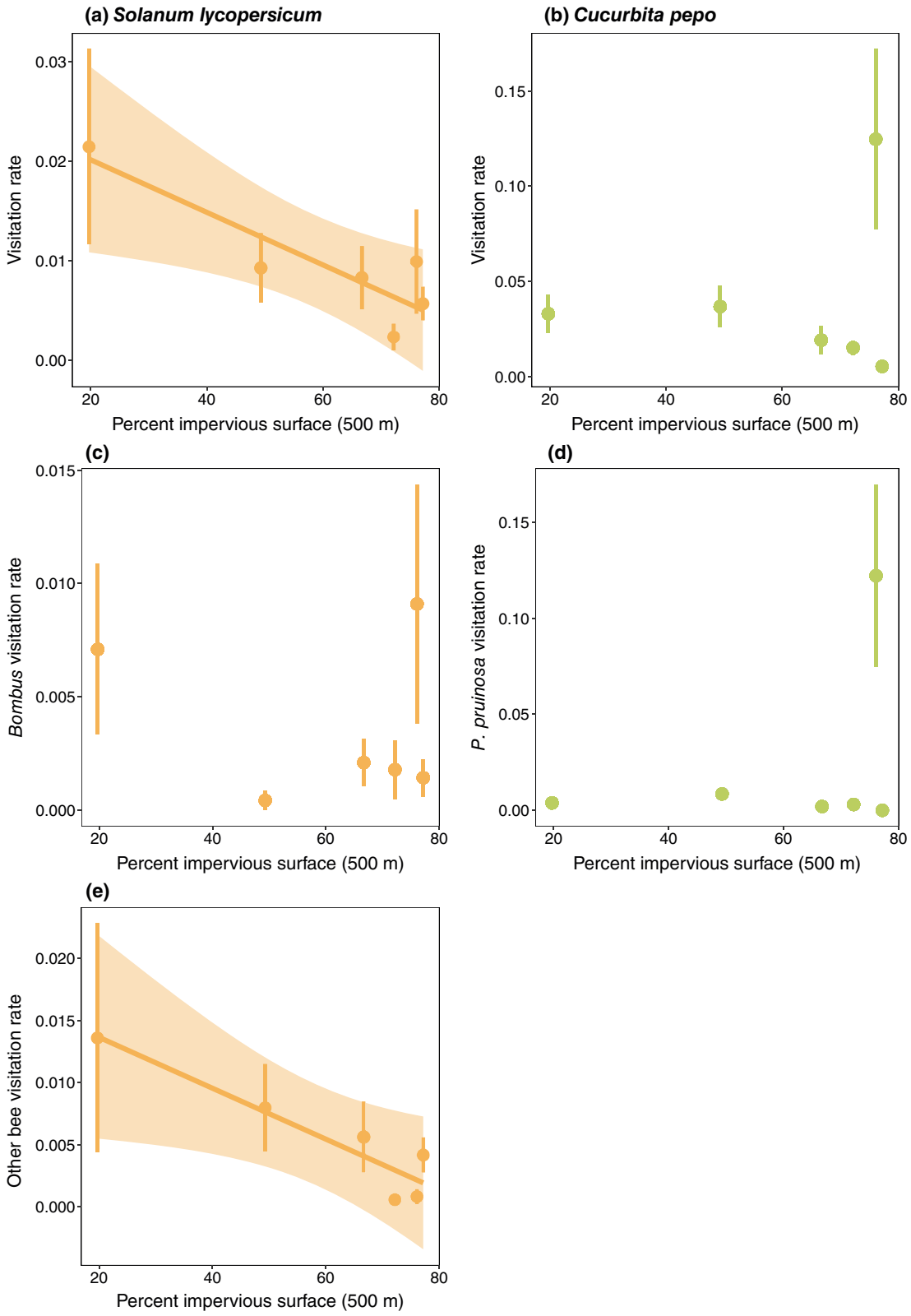

FIGURE 5 Pollinator visitation rate (visits per flower per minute) to *S. lycopersicum* (a) overall for all visitors, (c) by *Bombus* spp., and (e) by other bees, and to *C. pepo* (b) overall and (d) by squash bees (*Peponapis pruinosa*). Dots are site-level means and error bars SE. Error around lines of fit is SE.

Augochlora spp. are capable of buzz pollination and were frequently observed sonicating flowers on our study plants and more broadly across Chicago (Cardinal et al., 2018; Gruver & CaraDonna, 2021; Rosi-Denadai et al., 2020). In particular, the absence of *Agapostemon* in the four most urban sites (Appendix S1: Figure S2) may have contributed to this trend of decreasing visitation from small bees as urbanization increases, but this hypothesis requires further data collection to be evaluated. In an area where bee abundance was greater in urban than in nonurban sites, pollen limitation was still greater in urban areas for two of the three species studied, and this was linked to lower receipt of conspecific pollen for plants in the urban sites (Carper et al., 2014, 2022). These results coincide with patterns of bees in urban landscapes visiting a greater number of plant species overall, but a lower proportion of available plant species, likely due to greater plant richness (Baldock et al., 2015; Theodorou et al., 2017). Pollinator visit and search durations have also been shown to increase in urban areas, which could decrease overall visitation rates (Andrieu et al., 2009). Pollination services may also be changing in response to less studied abiotic characteristics of urbanization such as pesticide use, the urban heat island effect, or anthropogenic air pollution (Bloom et al., 2021; Descamps et al., 2021; Wenzel et al., 2020), which has been found to reduce floral visits by pollinators by as much as 83%–90% (Ryalls et al., 2022).

Some of our study pairs exhibited negative values for pollen limitation, indicating that control plants produced a higher proportion of fruits and/or more seeds than pollen-supplemented plants, primarily in *C. pepo*. A total of 16 *C. pepo* pairs had negative values for fruit set relative to controls (26.7% of pairs), and 10 pairs had negative values for seed set (35.7% of pairs). It is possible that we delivered an insufficient number of pollen grains or a lower quality of pollen compared to natural pollinators. These plants also might be resource- rather than pollen-limited so that the addition of extra pollen does not affect reproduction (Campbell, 1987; Campbell & Halama, 1993). However, we think this is unlikely because we consistently watered and fertilized all study plants. Finally, several *C. pepo* plants were infected by powdery mildew, and it is possible that pollen-supplemented plants with lower reproduction than controls had more severe infections. Fruit set was lower in *C. pepo* overall than in *S. lycopersicum*, and mildew infection might help to explain why, but this cannot be confirmed without further research. Regardless of why some pollen-supplemented *C. pepo* plants did not reproduce as well as control plants, we still find some support for the expected pattern of greater pollen limitation at more urban sites for *C. pepo* fruit set, despite the extra noise of the negative values.

Taken together, our results suggest that pollination deficits can increase with urbanization, and there are likely multiple interacting factors underlying this relationship. Understanding the drivers behind decreased pollination services in urban areas can help us develop best practices for improving pollination services in the future. Strategies for encouraging pollinator visitation to crops to increase yield could focus on providing habitat and planting resources that support a range of pollinators, particularly those that visit both specialist and generalist plant species, although the utility of these strategies needs to be empirically tested with data. Further research that considers multiple species across urbanization gradients and longer timescales, with additional local- and landscape-level factors, is necessary to understand the mechanisms behind the observed pollination deficits that increase with urbanization.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Zink et al., 2024) are available from Dryad: https://doi.org/10.5061/dryad.44j0zpcm6.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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