

Diversity of wild bees supports pollination services in an urbanized landscape

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Abstract Plantings in residential neighborhoods can support wild pollinators. However, it is unknown how effectively wild pollinators maintain pollination services in small, urban gardens with diverse floral resources. We used a ‘mobile garden’ experimental design, whereby potted plants of cucumber, eggplant, and purple coneflower were brought to 30 residential yards in Chicago, IL, USA, to enable direct assessment of pollination services provided by wild pollinator communities. We measured fruit and seed set and investigated the effect of within-yard characteristics and adjacent floral resources on plant pollination. Increased pollinator visitation and taxonomic richness generally led to increases in fruit and seed set for all focal plants. Furthermore, fruit and seed set were correlated across the three species, suggesting that pollination services vary across

the landscape in ways that are consistent among different plant species. Plant species varied in terms of which pollinator groups provided the most visits and benefit for pollination. Cucumber pollination was linked to visitation by small sweat bees (*Lasioglossum* spp.), whereas eggplant pollination was linked to visits by bumble bees. Purple coneflower was visited by the most diverse group of pollinators and, perhaps due to this phenomenon, was more effectively pollinated in florally-rich gardens. Our results demonstrate how a diversity of wild bees supports pollination of multiple plant species, highlighting the importance of pollinator conservation within cities. Non-crop resources should continue to be planted in urban gardens, as these resources have a neutral and potentially positive effect on crop pollination.

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Introduction

Biodiversity influences the provision of ecosystem services in a variety of semi-natural landscapes (Hooper et al. 2005). However, this has rarely been evaluated in cities (Bolund and Hunhammar 1999), where the vast majority of people now live (Seto et al. 2012). While the biological insurance hypothesis predicts a stabilizing effect of species richness on ecosystem services (Naeem 1998; Hooper et al. 2005; Tilman et al. 2006), abundance and species richness of a variety of taxonomic groups often decrease with urbanization (McKinney 2008), suggesting that some ecosystem services may be impaired in heavily urbanized landscapes. Alternatively, ecosystem services may still be maintained in cities if key species remain abundant despite

overall reductions in species richness. A more thorough understanding of the factors that influence provisioning of urban ecosystem services may directly benefit increasing human populations in cities.

Bees are considered mobile ecosystem service providers (Kremen et al. 2007) which increase yield of many crops globally (Klein et al. 2007), including many that are commonly grown in urban community and residential gardens (Matteson and Langellotto 2009). Although the scale of residential gardens usually is limited to home consumption, these sites account for as much as 6 % of global food production (Thebo et al. 2014) and comprise nearly 90 % of agricultural space in Chicago, IL, USA (Taylor and Lovell 2012). One species, the European honey bee *Apis mellifera* L., 1758, is often considered the most important pollinator for agriculture, but an increasing number of studies demonstrate the value of bee diversity to maintain or exceed pollination provided by commercial honey bee hives (Garibaldi et al. 2013; Mallinger and Gratton 2015). Honey bees often are less abundant in cities than outlying areas (McIntyre and Hostetler 2001; Cane et al. 2006; Leong et al. 2014), suggesting that cities may provide an opportunity to assess the ability of wild bees to sustain urban pollination services.

Although bee richness is often reduced in urban relative to semi-natural landscapes (Ahrne et al. 2009; Banaszak-Cibicka and Zmihorski 2011; but see Fortel et al. 2014), a number of wild bees have been documented in many urban habitats (Frankie et al. 2005; Fetridge et al. 2008; Matteson et al. 2008). In Chicago, we have documented 68 species in the heavily developed neighborhoods of the city and 138 in the broader region (K.C.M., unpublished data). Surprisingly, bee abundance and richness increased in the more densely populated neighborhoods of Chicago, potentially due to the propensity of humans to plant flowers for aesthetic purposes (Lowenstein et al. 2014). This suggests that increased floral resources may partially mitigate other potential negative effects of urbanization such as increased impervious surface. However, it is unclear if abundant floral resources around urban gardens facilitate pollination of all plants (e.g., Moeller 2004) or if they inhibit pollination of less attractive plants due to increased competition for pollinators (e.g., Kwak et al. 1998; Hennig and Ghazoul 2011). Nonetheless, multi-species floral arrays that attract a diverse pollinator assemblage (Ghazoul 2006) are expected to enhance pollination of plants with varying floral characteristics.

Directly measuring fruit and seed set in urban landscapes is challenging due to variation among sites in what plants are already grown and limited space for experimental plantings. Floral visitation is often used as a proxy of pollination (Vázquez et al. 2005), but is not entirely accurate because pollinators vary in their effectiveness at transmitting pollen



Fig. 1 ‘Mobile garden’ urban pollination trial including 9 flowering potted plants (3 focal species) brought to 30 residential yards to assess pollination services across the city of Chicago

(Rader et al. 2009). Even in cases of reduced floral visitation, pollination may be sufficient for maximum seed or fruit set (Ricketts et al. 2008). Furthermore, increased floral visitation may result in reduced seed or fruit set if more heterospecific than conspecific pollen is deposited (Leong et al. 2014). Therefore, we utilized a temporary ‘mobile garden’ (a standardized floral display including three plant species that varied in pollinator attraction and dependence) to assess pollination services in 30 residential yards in and around Chicago. This design examines pollination across a range of habitats, while standardizing the floral display and soil conditions (Samnegard et al. 2011; Williams and Winfree 2013). We hypothesized that fruit and seed set would differ for each focal plant species due to discordant dependence on, and attraction of, different insect pollinators. We also predicted that a richer surrounding floral community and a more diverse pollinator community would enhance pollination of focal plants.

Materials and methods

Sample design and study locations

We measured pollination in the field using groupings of nine plants in 2-gallon (7.57-L) pots, hereafter referred to as a mobile garden (Fig. 1). Each mobile garden consisted of three mature cucumber plants (*Cucumis sativus*, var. ‘Picklebush’), three mature eggplant plants (*Solanum melongena*, var. ‘Black Beauty’), and three mature purple coneflower plants (*Echinacea purpurea*, var. ‘Magnus’).

We choose these plants because their size and form are compatible with transportation to and placement at our field locations. Additionally, the plants vary in their dependence on and ability to attract pollinators, allowing an assessment of the consistency of ecosystem services in gardens with different floral resources and pollinator communities. Cucumber, a monoecious plant, is highly dependent on pollination from honey bees and other generalist pollinators (Stanghellini et al. 1997; Lowenstein et al. 2012) and produces small and misshapen or no fruits from self-pollination (Kauffeld and Williams 1972). Eggplant has hermaphroditic flowers that do not provide nectar and whose pollen is best released by buzz pollination of bumble bees (Free 1993). Self-incompatibility occurs in the genus *Echinacea* (Wagenius 2004), which is highly attractive to a broad range of pollinators (Lowenstein et al. 2014). In a preliminary trial for this project, we bagged flowers to keep pollinators away. Three percent of bagged cucumber flowers produced fruit, and 12.5 % of bagged eggplant flowers produced fruit, confirming the dependence of these plants on insect pollination.

Prior to each pollination trial, we standardized the number of open flowers in the mobile garden such that cucumber had 6–9 female flowers and a 2:1 ratio of females to males, eggplant had 5–9 flowers, and purple coneflower had 6–9 flower heads with pollen on receptive florets. Before and after trials, plants were grown in a greenhouse enclosed in <1-mm-mesh netting to prevent any insect visitation. Plants were then dropped off at study sites during partly to mostly sunny conditions when a similar weather pattern was expected (≥ 50 % of the duration) for the next 72 h.

The mobile garden was transported to 30 residential yards in and around Chicago for 72 h pollination trials. Twenty-four yards were in the city of Chicago; the remaining yards were spread over five nearby suburbs, all of which were in Cook County and would be considered urban neighborhoods. The mean distance between yards was 3.0 km (range 1.3–6.6 km). We measured land cover types within yards and calculated their percentage out of the entire outdoor space (i.e. yard), obtained from Google Earth area measurements. On average (\pm SE), yards were 136.8 ± 25 m²; all yards had a combination of green areas (turf grass and garden beds; mean \pm SE = 52.3 ± 3 % of yard area) and impervious surfaces (mean \pm SE = 46.3 ± 3.3 % of yard area). All yards had a protected outdoor space receiving direct sunlight and did not have honey bee hives or an immediate neighbor with bee hives. We asked all residents to complete a survey describing features in their yard such as vegetable gardens or insecticide application that could affect pollinators (Supplementary Table S1). We conducted pollination trials during two sampling periods: early summer

(14 June–8 July 2013) and mid-summer (25 July–9 August 2013). Our first experimental group of plants was adversely affected by greenhouse pests after field pollination trials. Therefore, while we report pollinator observations for both sampling periods, we only report fruit and seed set for the second sampling period.

Quantifying pollinator visitation and floral resources

We observed pollinator visits to the mobile garden for 30 min immediately after plants were placed in yards to record the amount of time until the first pollinator visited a mobile garden flower, hereafter referred to as recruitment time. Recruitment time provides a measure of how quickly pollinators are recruited to a new resource and could be an indicator of pollination outcomes. An additional 30 min of observation occurred on a separate day within the 72-h pollination trial, for a total of 60 min of observation per pollination trial. In addition to bees, hover flies (Syrphidae: Diptera) were included in observations, since they enhance pollination of flowers with accessible reproductive parts (Fontaine et al. 2005). Pollinators were identified by D.M.L. in the field to the genus level or to the species level for bumble bees and other identifiable bees.

During pollination trials, we also counted all flowers on shrubs and herbaceous plants in the backyard. We counted inflorescences, racemes, umbels, and spikes of flowers as single floral units for the purpose of estimating floral abundance. Although this method cannot account for differences in floral quality, and underestimates the actual number of flowers and florets, it is common to pool flowers as a ‘unit’ when analyzing their influence on pollinators (Carper et al. 2014; Baldock et al. 2015). We standardized floral richness at the genus level. To eliminate confounding effects with yard area and flowers in adjacent yards, we standardized floral abundance and richness by yard area for all analyses but refer to them simply as ‘floral density’ and ‘floral richness’ from here on.

Quantifying fruit and seed set

After the 72-h field pollination trial, we returned the mobile garden plants to the greenhouse and kept them under netting until all flowers that had been open at the sites had dropped or closed. Three weeks after each pollination trial, we harvested all cucumber and eggplant fruits and measured seed set (seeds per fruit) and fruit set (proportion of open flowers that produced fruit). For cucumber, we calculated fruit set as the number of fruits per female flower, and we counted the number of visibly developed seeds after cutting fruits in half lengthwise. To count eggplant seeds, we cut the fruit in half lengthwise and extracted and counted all seeds from one randomly selected half.

We used a different technique to measure pollination of purple coneflowers. The flower heads on these plants have concentric rows of florets that open from bottom to top (see Wagenius 2004 for morphology of a congeneric species). A lack of style shriveling (i.e., "style persistence") in receptive florets indicates insufficient pollination. We examined style persistence 24 h after plants were returned from each site and estimated the percentage of receptive styles that had shriveled on each flower head, using 25 % increments. We then averaged this value over all flower heads that were open during the pollination trial. For simplicity, we refer to this measure as purple coneflower fruit set hereafter.

Statistical analyses

We compared the observed number of visits and richness of pollinators at each of the three mobile garden plant species using Kruskal–Wallis tests. We used Pearson's correlations to determine if seed and fruit set were correlated among and between the three focal plants. We also evaluated the relationship between fruit and seed set of each focal plant species and pollinator visits to the mobile garden, pollinator richness at the mobile garden, pollinator visits to each mobile garden plant species, and recruitment time. Finally, we used Pearson's correlations to determine if the number of observed visits to the mobile garden by specific pollinators was positively correlated with fruit or seed set. Specifically, we evaluated visitation from the following four common groups: bumble bees (*Bombus* spp.), honey bees (*Apis mellifera*), yellow-faced bees (*Hylaeus* spp.), and sweat bees [*Agapostemon* spp., *Augochlora pura* (Say 1837), *Halictus* spp., and *Lasioglossum* spp.]. To improve normality of cucumber seed set, we added 1 and log-transformed the sum prior to analysis.

To evaluate differences in the suite of pollinators that visited each plant species, we used multi-response permutation procedures (MRPP; Mielke 1991). MRPP is a non-parametric procedure that uses the species occurrence matrix and a grouping variable (in this case, plant species) to test the hypothesis that species composition differs between groups. The statistic A describes within-group homogeneity compared to random expectation, and is highest ($A = 1$) when all species are identical within groups (i.e., within-group homogeneity is high). We used indicator species analysis (Tichý and Chytrý 2006) to identify pollinator species that are particularly "faithful" visitors to each plant species. The phi coefficient for indicator analysis ranges from -1 (for a perfect negative indication) to $+1$ (for a perfect positive indication). Pollinator species would be perfect indicators of a plant species if they always visited that plant and never visited other plants. MRPP and indicator species analysis were computed in PC-ORD v.6 (McCune and Mefford 2011).

We used independent t tests to evaluate the effect of insecticide application and non-focal mobile garden plants on pollinator visits and richness to the mobile garden. To investigate the effect of mowing frequency on mobile garden pollinators, we used regression with negative binomial distribution.

Modeling pollination services

To investigate the influence of pollinator visitation and backyard flowers on pollination services, we created linear models for each mobile garden plant species with the following response variables: cucumber fruit set, cucumber seed set, eggplant fruit set, eggplant seed set, and purple coneflower fruit set. We used best-subsets regression to identify pollinator activity metrics that predicted each pollination response variable. Using AICc, we then compared the best performing model to one that also included backyard floral richness or density (selecting the measure that was most highly correlated with the response variable). This allowed us to test the hypothesis that surrounding floral resources have an additional effect on pollination of focal plants, beyond the effect they have on abundance or richness of the pollinator community. Analyses were performed using R v.2.15 and package AICcmodavg (R Development Core Team 2012; Mazerolle 2013). Prior to analyses, all variables were checked for normality, and cucumber seed set was log-transformed. Alpha was set at 0.05 for all statistical tests.

Results

In total, across the 30 field locations and two sampling periods, we observed 1320 visits by at least 20 pollinator taxa to the mobile garden plants (Table 1). On average (\pm SE), each mobile garden received 22.0 ± 2.2 visits by 4.2 ± 0.3 pollinator taxa. Certain insect pollinators were frequent visitors to the mobile gardens. These included hover flies (*Toxomerus*, 21 % of visits), the common eastern bumble bee *Bombus impatiens* Cresson 1863 (16 %) and a genus of sweat bees (*Lasioglossum* spp. 15 %). The European honey bee made up just 6.7 % of observed visits to focal plants. The recruitment time before the first pollinator visited the mobile garden ranged from 1 to 30+ min, with a mean time (\pm SE) of 9.3 ± 1.5 min. When first visiting the garden, pollinators most frequently landed on purple coneflower (57 % of total visits). *Toxomerus* spp. and *Lasioglossum* spp. were the first pollinators to visit plants in 52 % of sites.

Pollinators and pollination services

The number of pollinator visits to each plant species differed significantly ($H = 41.84$, $P < 0.001$; Fig. 2) with

Table 1 Number of observed visits of pollinator taxa to each mobile garden plant species

Pollinator	Visits to cucumber	Visits to eggplant	Visits to purple coneflower
<i>Agapostemon virescens</i>	7	3	136 ^a
<i>Andrena</i> spp.	0	0	4
<i>Anthidium manicatum</i>	4	0	7
<i>Apis mellifera</i>	72	3	13
<i>Augochlora pura</i>	3	0	0
<i>Bombus bimaculatus</i>	0	3	16
<i>B. griseocollis</i>	0	3	28 ^a
<i>B. impatiens</i>	104	44	61
<i>Bombus</i> spp.	1	0	1
<i>Halictus</i> spp.	0	0	21 ^a
<i>Hylaeus</i> spp.	47	17	30
<i>Lasioglossum</i> spp.	128 ^a	16	55
<i>Megachile</i> spp.	2	0	43 ^a
<i>Melissodes bimaculata</i>	21	4	5
<i>Melissodes</i> spp. ^b	0	0	118 ^a
<i>Sphecodes</i> spp.	1	0	0
<i>Stelis</i> spp.	0	0	3
<i>Syrphus</i> spp.	3	2	8
<i>Toxomerus</i> spp.	162	11	101 ^a
<i>Xylocopa virginica</i>	0	3	6

Plants were observed for two 30-min intervals at each site ($n = 30$) during two separate sampling periods

^a Pollinators that were significant indicator species for a particular plant species

^b All species of *Melissodes* excluding *M. bimaculata*

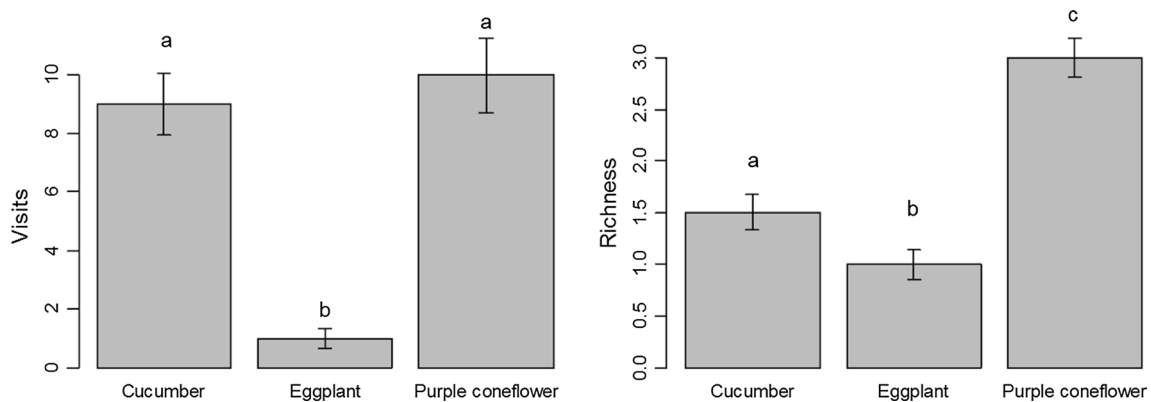


Fig. 2 Median number of pollinator visits and pollinator taxonomic richness to each mobile garden plant species (+SE) across all trials. Letters indicate significant differences at $P < 0.05$

more pollinators visiting both purple coneflower and cucumber ($P < 0.05$) than eggplant. There also was a significant difference in the taxonomic richness of pollinator visitors to each plant species ($H = 41.63$, $P < 0.001$) with richness being highest on purple coneflower ($P < 0.05$), followed by cucumber ($P < 0.05$), and then eggplant ($P < 0.05$). Despite differences in pollinator visitation and richness, all three plants produced fruit and seed at most

sites (Table 2). Eggplant fruit and seed set were significantly correlated with each other ($r = 0.45$, $P < 0.01$), as were cucumber fruit and seed set ($r = 0.53$, $P < 0.001$). Furthermore, with the exception of eggplant fruit set, which was not correlated with pollination of any other plants, pollination measures tended to be correlated among the three different plant species (Supplementary Table S2).

Table 2 Average seed and fruit set (\pm SE) for each mobile garden plant species

Plant	Fruit set (% of total open flowers)	Fruits produced per mobile garden	Seed set
Cucumber	42.7 \pm 4.6	3.2 \pm 0.4	28.2 \pm 5.1
Eggplant	48.2 \pm 4.1	3.1 \pm 0.4	227.1 \pm 18.8
Purple coneflower	40.9 \pm 4.3		

Table 3 Pearson's correlation coefficients (r) of pollinator visitation metrics and floral resources with pollination services ($n = 30$)

Pollinator visitation metrics	Cucumber fruit set	Cucumber seed set	Eggplant fruit set	Eggplant seed set	Purple coneflower fruit set
Pollinator richness at mobile garden	0.39*	0.04	0.37*	0.14	0.56***
# of visits to mobile garden	0.54**	0.25	0.10	0.53*	0.43*
# of visits by <i>Apis mellifera</i>	0.32	0.26	0.16	0.18	0.40*
# of visits by <i>Bombus</i> spp.	0.28	-0.07	0.17	0.50**	0.30
# of visits by <i>Hylaeus</i> spp.	0.40*	0.17	0.23	0.19	0.21
# of visits by Halictidae	0.46*	0.29	-0.06	0.38*	0.37*
# of visits by Syrphidae	0.54*	0.03	0.09	0.53**	0.43*
# of visits to focal plant	0.62***	0.42*	0.19	0.41*	0.28
Recruitment time	-0.43**	-0.17	-0.17	-0.18	-0.33
Backyard floral resources					
Floral density	0.06	-0.16	-0.13	-0.14	0.36*
Floral richness	-0.09	0.02	-0.23	-0.12	0.16

Cucumber seed set was transformed prior to analysis by adding 1 and log-transforming the sum

Halictidae includes bees in the genera *Agapostemon*, *Augochlora*, *Halictus*, and *Lasioglossum*

Values in bold are significant at * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

At least one measure of pollinator activity was positively associated with seed and fruit set in each plant (Table 3). Cucumber seed and fruit set were best predicted by number of visits to cucumber plants, eggplant and purple coneflower fruit set were best predicted by pollinator richness at the mobile garden, and eggplant seed set was best predicted by number of visits to the mobile garden.

Individual plants varied in terms of which specific pollinator groups were most attracted to them ($A = 0.10$, $P < 0.001$) and which pollinator groups were linked with fruit and seed set. Cucumber was disproportionately visited by *Lasioglossum* spp. (Table 1), and sweat bee visitation to the mobile garden (mostly *Lasioglossum* spp.) was positively correlated with cucumber fruit set ($r = 0.46$, $P = 0.01$; Table 3). The number of yellow-faced bee visits to the mobile garden was also positively correlated with cucumber fruit set ($r = 0.40$, $P = 0.03$). Despite the fact that no pollinator taxa were significant indicators of eggplant (Table 1), eggplant seed set was correlated with the number of bumble bee ($r = 0.50$, $P = 0.005$) and sweat bee visits to the mobile garden ($r = 0.38$, $P = 0.04$; Table 3). Several pollinator taxa were disproportionately associated with purple coneflower (Table 1), but purple coneflower fruit set was only positively correlated with the number of honey bee ($r = 0.40$, $P = 0.03$) and sweat bee visits ($r = 0.37$, $P = 0.04$).

Influence of backyard features and floral resources

Vegetable gardens were present in 57 % of sample sites ($n = 17$), and insecticide was applied at 20 % of sites ($n = 6$). Pollinator visits ($t = 0.20$, $P = 0.84$) and richness ($t = 0.61$, $P = 0.54$) at the mobile garden did not differ at sites with vegetable gardens. Similarly, neither pollinator visits ($t = -0.17$, $P = 0.89$) nor richness ($t = 0.07$, $P = 0.92$) differed at homes that used insecticide during the summer. The frequency of mowing per month did not affect pollinator visits ($\beta = -0.03$, $P = 0.73$) or richness ($\beta = 0.06$, $P = 0.45$) at the mobile garden.

The sampled yards contained an average (\pm SE) of 885 \pm 129 floral units and 15 \pm 1.2 flower genera (Supplementary Table S3). Standardized by area, mean floral density was 7.15 \pm 1.2 flowers and mean floral richness was 0.16 \pm 0.02 genera per square meter. Floral density and richness were correlated with each other ($r = 0.71$, $P < 0.01$). Non-focal purple coneflower had no effect on mobile garden purple coneflower fruit set ($P = 0.46$). There was a marginal reduction ($P = 0.07$) in mobile garden cucumber fruit set and no reduction in seed set ($P = 0.96$) from non-focal cucurbits. Only one site had non-focal eggplant, precluding an analysis of this effect on mobile garden eggplant reproduction. For cucumber and eggplant, the

Table 4 Models of pollination services for each mobile garden plant, ranked by AIC_c

Pollination services	Model no.	Coefficients and significance of predictor variables		AIC _c	R ²
		Pollinator visitation	Floral resources		
Cucumber fruit set	1. Visits to cucumber	0.014*		−5.49	0.38*
	2. Floral richness	0.014*	−0.061	−2.85	0.38*
Cucumber seed set	1. Visits to cucumber	0.063*		114.06	0.18*
	2. Floral richness	0.065*	−0.047	115.42	0.22*
Eggplant fruit set	1. Pollinator richness at mobile garden	0.048*		−1.45	0.13*
	2. Floral richness	0.046*	−0.427	−0.37	0.18
Eggplant seed set	1. Number of visits to mobile garden	3.183*		360.15	0.28*
	2. Floral density	3.356*	−3.416	360.92	0.33*
Purple coneflower fruit set	1. Pollinator richness at mobile garden	7.715*		270.29	0.32*
	2. Floral density	7.134*	1.017	269.51	0.39*

Model 1 included the pollinator visitation metrics identified by best subsets regression

Model 2 included the pollinator visitation model and the most explanatory floral resource variable

Cucumber seed set was transformed prior to analysis by adding 1 and log-transforming the sum

* Indicates coefficients and regression models that were significant at $P < 0.05$

best supported models only included pollinator visitation. On the other hand, floral density increased the explanatory power of the model of purple coneflower fruit set (Table 4).

Discussion

We found a diversity of pollinators in Chicago backyards. Unlike many agricultural landscapes, where European honey bees can comprise 50 % of all flower visitors (Garibaldi et al. 2011), only 7 % of mobile garden visitors were honey bees. Our findings suggest that wild bees make important contributions to pollination services in urban areas. A diversity of wild insect pollinators may increase seed and fruit set through complementary placement of pollen on stigmas, temporal variation in flower visitation (Chagnon et al. 1993; Hoehn et al. 2008), and beneficial behaviors such as sonication by bumble bees. Pollinator diversity should also, theoretically, help stabilize pollination service in disturbed landscapes, although this remains to be empirically demonstrated (Cariveau et al. 2013).

At a plant community level, pollinator diversity is important in attracting the most efficient pollinators for each flower type and thus enhancing yield (Klein et al. 2003; Hoehn et al. 2008). At the mobile garden, each focal plant also benefitted from a different suite of pollinators. Previous work supports our findings that bumble bees enhance eggplant seed set (Abak et al. 1995), as they effectively buzz pollinate flowers. We also observed a positive correlation between sweat bee visits to the mobile garden and eggplant seed set. However, unlike bumble bees, sweat bees are not known to buzz pollinate. Bumble bee and

sweat bee visits to the mobile garden were correlated with each other ($r = 0.50$, $P < 0.01$), and we believe that this is the likely explanation for the correlation between sweat bees and eggplant pollination.

Pollinators may influence fruit and seed set in different ways (Ne'eman et al. 2010). In particular, fruit set may indicate simple presence/absence of pollinator visits (Pellissier et al. 2012), whereas seed set may be a better indicator of total pollen transfer by particular pollinators (Medrano et al. 2009). We found pollinator visits to best explain fruit set in cucumbers but seed set in eggplant. Cucumber flowers are imperfect but monoecious, so transfer of pollen by an insect vector is required to set any fruit. On the other hand, eggplant has perfect flowers, and some eggplant flowers may have self-pollinated by wind. While wind may have contributed to eggplant fruit set, buzz pollination from bumble bees would further increase seed set. The correlations between multiple pollinator taxa and pollination services support the idea that fruit maturation was primarily due to cross-pollination by insects. However, we acknowledge that some mobile garden fruits may have resulted from self-pollination, especially in eggplant. Future researchers of urban pollination services should consider bagging some flowers to demonstrate the degree to which insect visitation enhances pollination beyond any self-fertilization.

Even when pollinator abundance is high, seed set can be limited by bees that visit flowers but do not transfer pollen (Ksiazek et al. 2012). Most of the insects initially recruited to the mobile garden, during the first 30-min observation period, were smaller-bodied sweat bees and hover flies. If small-bodied pollinators were the dominant visitors outside

of our observation period, this could have reduced seed production in cucumber and eggplant. However, faster recruitment times were linked to increased visitation to the mobile garden and even enhanced cucumber fruit set. Furthermore, the most faithful visitors to mobile garden plants were not always the first to visit gardens. Cucumbers were most commonly visited by smaller-bodied bees, which carry fewer pollen grains and have different pollen-collection behavior than larger-bodied bees (Hoehn et al. 2008). Because a minimum amount of pollen deposition is required for successful fruit set, visitation by smaller bodied bees may increase the likelihood of fruit production even when total pollen transfer, and resulting seed set, is minimal. Other visitors may bring pollen grains from other plant species. The small size of plant populations in our mobile garden means that fewer conspecific pollen grains are available for transfer between plants (Cheptou and Avendano 2006; Pellissier et al. 2012). As Verboven et al. (2014) aptly noted, the negative effect of the urban matrix on seed set is not easily separated from the effect of small population size on plants.

Unlike cucumber and eggplant, the number of pollinator visits to purple coneflower was not a good indicator of pollination. Instead, fruit set was best explained by pollinator richness. The model of coneflower pollination was further improved by adding backyard floral resources. We explain this in several ways. First, self-incompatibility in *Echinacea* requires pollen from another plant for successful fertilization (Wagenius 2004). While most pollinators visited purple coneflower plants, a greater number of visits would only hasten style shriveling if pollen was exchanged between different plants. The small population of three potted plants reduced potential for pollen transfer between plants, even in the presence of non-focal *Echinacea* in backyards. Second, the diverse pollinator assemblage visiting purple coneflower could have provided variation in behavioral traits that influence pollen transfer and increased opportunity for visitation at times when pollen was accessible (Hoehn et al. 2008). Finally, pollinators in backyards quickly located purple coneflower and visited this species more frequently than cucumber or eggplant. This may explain how surrounding resources enhanced purple coneflower pollination beyond just increasing the potential pollinator pool.

While backyard floral resources had a positive effect on coneflower pollination, they had a neutral effect on eggplant and cucumber. Likely, this difference stems from the relative attractiveness of these flowers. Purple coneflower is highly attractive to a variety of pollinators (Lowenstein et al. 2014). Therefore, it might attract pollinators previously foraging on other backyard flowers and a high number of adjacent plants may benefit purple coneflower. However, less attractive flowers, such as eggplant and cucumber,

are visited by fewer bees and will benefit less from the presence of nearby flowers or vegetable gardens. Despite different visitation rates to mobile garden plant species, correlations among pollination measures of different plant species in the mobile garden indicate that insect-pollinated plants with different floral morphology respond similarly across varied environments.

To some degree, the facilitative, neutral, or inhibitive effects of other floral resources are likely to depend on context, such as spatial distribution of resources and other neighborhood effects (Werrell et al. 2009; Seifan et al. 2014; Waters et al. 2014). The legal boundaries of backyards are not a meaningful barrier to bees. Adjacent flowers in different yards could be as important as resources in the focal yard. While we did not record flowers in neighboring yards, neighborhood norms and socioeconomic factors tend to affect the design of yards (Luck et al. 2009; Nassauer et al. 2009) and it is likely that yards on a block would be similar to each other. Since larger-bodied pollinators can forage beyond the studied yards, practices in other yards that influence nest growth rates (Goulson et al. 2002) and foraging habitats may have also affected the pollinators visiting the mobile garden.

Despite identifying trends in pollinator visitation to mobile garden plants, we acknowledge the limitation of measuring pollination services over a single 72-h sample period. Sampling for additional periods would provide a more complete picture of environmental variation that might influence plant pollination and would not underestimate the pollination services provided by solitary bees with short flight seasons (Ricketts et al. 2008). However, we believe the 72-h sampling period was suitable, as flowers were open either entirely or for most of their duration at a study site. Cucumber flowers are only open for 24 h. Eggplant flowers can remain open for up to 5 days, but eggplant stigmas are most receptive on day 2 (Rao 1980). All eggplant flowers were in the yards on day 2 of opening. Coneflower pollen remains accessible for greater than 1 week, but we marked the rows of pollen that were available to pollinators while the plant was in the yard. Finally, mobile garden plants were taken to yards at a time they would typically be blooming so they could be visited by pollinators that would normally visit the three species.

Our findings add to a small but growing body of literature suggesting that wild bees may be important pollinators in urban areas (Cussans et al. 2010; Williams and Winfree 2013; Verboven et al. 2014; Leong et al. 2014; Potter and LeBuhn 2015). Urban residential yards and gardens present a particularly interesting puzzle for plant reproduction. The loss of stable forage in urban areas and the potential for pollinator visits to heterospecific plants in a small area could limit yield. However, relative to agricultural landscapes, residential gardens may be superior bee habitats

where pollination is enhanced (Cussans et al. 2010; Samnegard et al. 2011). Some studies demonstrate that highly efficient pollinators such as bumble bees respond positively to urban land use (Verboven et al. 2014), are abundant in urban community gardens (Matteson and Langellotto 2009), and benefit from artificial and natural nesting sites (Osborne et al. 2008). In turn, this benefits pollination of urban plants, even when they are located adjacent to other resources that potentially compete for pollinators. Our results suggest that urban garden plants are pollinated by a diverse array of wild pollinators. Co-occurring resources in gardens did not cause competition for pollination and may in fact lead to complementary visitation to adjacent plant species.

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Author contribution statement DML collected the data and performed most analyses. DML, KCM, and ESM conceived and designed the experiments. DML, KCM, and ESM wrote the manuscript.

Compliance with ethical standards

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed. All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

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