

**Insects in the City:**  
**Evaluating Pollination and Biological Control in Urban Neighborhoods**

BY

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THESIS

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DML

## Contribution of Authors

Chapter 1 is a published research article (Previously as Lowenstein, D. M., K. C. Matteson, and E. S. Minor. 2015. Diversity of wild bees supports pollination services in urbanized areas. *Oecologia* 179: 811-821). My research mentor, Emily Minor, and a collaborator, Kevin Matteson, contributed to the writing of this article.

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Chapter 3 is an unpublished article with Kevin Matteson and Emily Minor as coauthors. Kevin Matteson collected some of the data that were included in analyses.

Chapter 4 is an article submitted for publication to *Biological Control* with Emily Minor as a coauthor. Emily Minor contributed to the writing of this article.

Chapter 5 is an article submitted for publication to *Environmental Entomology* with Maryam Gharehaghaji and David Wise as coauthors. Maryam Gharehaghaji contributed to this article by helping with analysis and creating figure 1, and David Wise offered guidance in statistical analysis and writing.

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## THESIS SUMMARY

Urban areas are a challenging environment for flower-visiting and economically important arthropods. Frequent disturbance and habitat loss often reduce biodiversity (McKinney 2006) and alter community composition (Gagne and Fahrig 2011). Yet, it is an overstatement to suggest that the characteristics of urban areas are uniformly detrimental to all functional groups. Fine-scale variation in urban land cover (Cadenasso et al. 2007) creates local-level disparities in habitat quality. While habitat loss is more acute in cities compared to surrounding ecosystems, robust pollinator (Matteson et al. 2008, Leong et al. 2014) and natural enemy (Martinson and Raupp 2013, Gardiner et al. 2014) communities exist in urban areas. Both arthropod groups have adapted to disturbed conditions through changes to the dominant functional characteristics such as generalism in insect host selection (Kitahara and Fujii 1994, Bennett and Gratton 2012) and using artificial structures as a nesting cavity (Matteson et al. 2008). Since cities are a dynamically shifting entity influenced by social and economic forces, factors unrelated to biological variables can affect plants and arthropods. In the past few decades, deindustrialization in Midwest (USA) cities has increased the number of vacant lots and food production sites (Keating 2010, Taylor and Lovell 2012), adding a novel component to landscape composition.

Pollination from bees and prey suppression from natural enemies are two beneficial ecosystem services in residential gardens and urban agriculture. Pollinators are required for reproduction in a majority of crops (Klein et al. 2007) and wildflowers (Ollerton et al. 2011). Natural enemies provide biological control against herbivores. This alternative to insecticide is estimated at a four billion dollar (USD) value (Losey and Vaughan 2006). While pollinators and natural enemies are desirable by gardeners and growers, attracting a diverse group of beneficial insects requires suitable habitat and nectar and pollen (Steffan-Dewenter and Tschardt 2001,

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Potts et al. 2003, Isaacs et al. 2009, Blaauw and Isaacs 2012). Floral resources are distributed irregularly in cities and are influenced by socioeconomic factors and neighborhood characteristics (Hope et al. 2003, Mennis 2006, Grove et al. 2014). Since the floral preferences of natural enemies and pollinators differ between species, further efforts are needed to identify the drivers of floral community composition and functional traits. Consequently, patterns that influence floral characteristics or lead to an unequal distribution of resources could regulate the relationships with insect populations.

Biodiversity patterns in degraded habitats are relevant when examined in connection with ecosystem services. Ecologists have extensively studied the value of the biodiversity-ecosystem hypothesis (Srivastava and Vellend 2005) with evidence that diversity in function and species richness are associated with the success of biological control (Griffin et al. 2013) and pollination services (Hoehn et al. 2008, Brittain et al. 2013). However, the relationship between insect biodiversity and an ecosystem service can vary by species identity (Straub et al. 2008). In some cases, the presence of particular predator species (Wilby et al. 2005, Straub and Snyder 2006) rather than greater richness is more important for prey suppression. Similarly for pollination, specialized floral morphology in crops and wildflowers makes visits by certain pollinator species more effective than more visits from multiple species. The biodiversity-ecosystem function relationship is further confounded by habitat loss and decline of natural enemy diversity in cities (Denys and Schmidt 1998, Fenoglio et al. 2009, Bennett and Gratton 2012). Fewer natural enemy species could reduce biological control of crop pests. Alternatively, pests could be attacked by parasitoids and predators that tolerate the disturbed urban environment.

Human modification to the landscape warrants the inclusion of social characteristics to

## THESIS SUMMARY (continued)

identify the relationships between habitat complexity, insect populations, and ecosystem services. In particular, yard management practices and demographics may shape plant communities and higher level trophic interactions in a unique manner. It is vital to identify if certain urban characteristics make a neighborhood more susceptible to a decline of pollination services or biological control. In addition to evaluating the performance of ecological theory in the complex urban setting, this dissertation provides baseline data on two ecosystem services that are needed to further develop infrastructure for maximizing production and commercial sale of vegetables in urban agriculture. I employ an interdisciplinary approach to investigate biodiversity as well as plant-pollinator and predator-prey interactions in residential neighborhoods in the Chicago, IL metropolitan area.

Increased pollinator diversity often enhances plant reproductive output through complementary behavior and visitation (Fontaine et al. 2005, Hoehn et al. 2008). In chapter 1, I examined if pollinator species partition visits between three insect-pollinated plant species and how diversity affects yield in an equivalent floral array. Using a phytometer design, I evaluated if plant reproductive success is limited by inadequate pollinator diversity or competing resources in the spatially discrete area of residential yards. Each plant species varied in pollinator visitation and diversity, yet all experienced comparable fruit set and yield. The attractiveness of a plant may enhance reproduction, but less attractive species did not experience reduced fruit production. Furthermore, there was a positive effect of floral abundance on purple coneflower seed set, where the most attractive plant gained visitors by being located in a rich floral community. This study suggested that efficient pollinators remain in urban areas and provide sufficient pollination to a diverse group of plants.

## THESIS SUMMARY (continued)

Urban neighborhoods vary in demographic characteristics and development intensity. These social factors can influence floral abundance (Hope et al. 2003), and, in chapter 2, I investigated patterns in floral attributes and beta diversity in 58 urban, residential neighborhoods. I identified that most flowering plants belonged to ornamental cultivars introduced by humans and were non-native to the Midwest region. Most plants species occurred infrequently, and there was high turnover in ornamental plants, suggesting that cultivated plants drive beta diversity. Interestingly, I found a hump-shaped pattern where plant species richness was greatest in areas of intermediate Hispanic populations and development intensities. These findings suggest that areas with ethnically diverse residents and moderate level of urbanization have the greatest resource diversity in cities. Although the additional residences may be associated with increased impervious surfaces, the variety of garden management practices allows for an efficient use of remaining green spaces to introduce novel plant species.

In chapter 3, I build on the previous chapter by investigating plant-pollinator visitation across neighborhoods. Since the composition of flowering plants is skewed towards non-native and perennial species, I examined if most pollinator visits were limited to species with these attributes. Additionally, I investigated network-level assembly. I identified that a small number of frequently occurring plants supply resources for the majority of pollinating insects. On average, perennial plant species received the highest pollinator visitation rate, but native plants had a greater average visitation rate than non-natives. Nonetheless, non-native super-generalist weedy and ornamental species influenced network structure through a non-nested pattern and a low number of connected links. Most pollinator taxa were generalist foragers, but I found some specialization that was dependent on temporal patterns and the energetic costs of foraging. This

## THESIS SUMMARY (continued)

chapter indicated that non-native plants have integrated into the pollination network, but that these abundant non-native species may not serve as the ideal resource for pollinators.

In chapter 4, I studied the resource concentration hypothesis and contributed to the debate regarding top-down or bottom-up control as the primary mediator of herbivore populations. I examined this theory in urban agriculture, a novel habitat with high plant biomass relative to immediately surrounding areas. By selecting three scales of food production, I investigated if patch size or the natural enemy community had a greater effect on herbivore populations and herbivory in brassica. Herbivore abundance and plant damage were similar each food production scale, and a rich predator and parasitoid community was associated with a decline in cabbageworm and aphid abundance. This chapter demonstrated that urban agriculture is a structurally complex habitat that functions similarly to more intact system in the strength of top-down control. Urban food production provides insect and floral resources, which in turn support a robust natural enemy community that regulates herbivore populations.

In chapter 5, I quantified cabbage looper mortality across each agricultural scale and evaluated the influence of within-garden factors and surrounding landscape affect biocontrol of cabbage loopers. I evaluated biological control using cabbage looper, a specialized caterpillar pest that defoliates brassica. In a laboratory assay, I also analyzed the effectiveness of several predator taxa at consuming cabbage looper eggs and larvae. On average, 54% of sentinel eggs and 25% of larvae were removed by natural enemies. Yet, mortality rates were similar comparable across food production scales and the urban landscape. The only significant relationship was a weak negative effect of defoliation on egg suppression. This work identified that natural enemies contribute to prey suppression in a cultivated crop family and that landscape

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and local factors have poor predictive power low in urban agriculture.

By researching biodiversity within cities, I identified how fine-scale variation in landscape, local, and social factors mediate plant, pollinator, and natural enemies in densely populated areas. This work documented diverse natural enemy and pollinator communities and offers a positive outlook for gardens and urban agriculture. Both functional groups in this study, pollinators and natural enemies, provide ecosystem services with commercial value for crop production. However, the unequal use of floral resources by pollinators suggests that private citizens as well as municipal entities should focus plant enhancement efforts in specific neighborhoods whose socioeconomic characteristics make them prone to limited floral richness. The baseline data regarding pest suppression supports the value of natural enemies as a component for urban food production. Further studies that investigate patterns in specialized arthropod populations are essential to identify the intersection of theory and applied science for conservation efforts in cities.

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## **Chapter I. Diversity of wild bees supports pollination services in urbanized areas**

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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—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 crop 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.

## **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. Alternately, 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) that 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. (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 (unpublished data KCM). 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 (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, Illinois (USA). 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.

## **Methods**

### *Sample design and study locations*

We measured pollination in the field using groupings of nine plants in 2-gallon pots, hereafter referred to as a mobile garden (Figure 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 1973). 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 ( $\geq 50\%$  of the duration) for the next 72 hours.

The mobile garden was transported to 30 residential yards in and around Chicago for 72-hour 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 of 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  $136.8 \pm 25$  m<sup>2</sup>; all yards had a combination of green areas (turf grass and garden beds; mean  $\pm$  SE =  $52.3 \pm 3\%$  of yard area) and impervious surfaces (mean  $\pm$  SE =  $46.3 \pm 3.3\%$  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 (Appendix 1). 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 minutes 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 minutes of observation occurred on a separate day within the 72-hour pollination trial, for a total of 60 minutes 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 DML 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 flowering 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 hour 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 hours 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 and 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 version 2.15 and package AICcmodavg (R Development Core 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  $22.0 \pm 2.2$  visits by  $4.2 \pm 0.3$  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 1-30+ minutes, with a mean time ( $\pm$  SE) of  $9.3 \pm 1.5$  minutes. 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 ( $H = 41.84$ ,  $P < 0.001$ ; Figure 2) with 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 (Appendix 2).

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 (*Hylaeus* spp.) 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 (Appendix 3). 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 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 also, theoretically, should 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-minute 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 deposit 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, 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-hour 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-hour 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 hours. Eggplant flowers can remain open for up to five days, but eggplant stigmas are most receptive on day two (Rao 1980). All eggplant flowers were in the yards on day two of opening. Coneflower pollen remains accessible for greater than one 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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## TABLES

Table 1. Number of observed visits of pollinator taxa to each mobile garden plant species. Plants were observed for two 30 minute intervals at each site (n = 30) during two separate sampling periods. Asterisk (\*) shows pollinators that were significant indicator species for a particular plant species.

Pollinator	Visits to cucumber	Visits to eggplant	Visits to purple coneflower
<i>Agapostemon virescens</i>	7	3	136*
<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*
<i>B. impatiens</i>	104	44	61
<i>Bombus</i> spp.	1	0	1
<i>Halictus</i> spp.	0	0	21*
<i>Hylaeus</i> spp.	47	17	30
<i>Lasioglossum</i> spp.	128*	16	55
<i>Megachile</i> spp.	2	0	43*
<i>Melissodes bimaculata</i>	21	4	5
<i>Melissodes</i> spp.#	0	0	118*
<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*
<i>Xylocopa virginica</i>	0	3	6

# - All species of *Melissodes* excluding *M. bimaculata*

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). 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*. Bolded values are significant at  $P < 0.05$ : \*:  $P < 0.05$ , \*\*:  $P < 0.01$ , \*\*\*:  $P < 0.001$

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

Table 4. Models of pollination services for each mobile garden plant, ranked by AIC<sub>c</sub>. 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.

Pollination services	Model #	Coefficients and significance of predictor variables		AIC <sub>c</sub>	R <sup>2</sup>
		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*

## FIGURES



Figure 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.

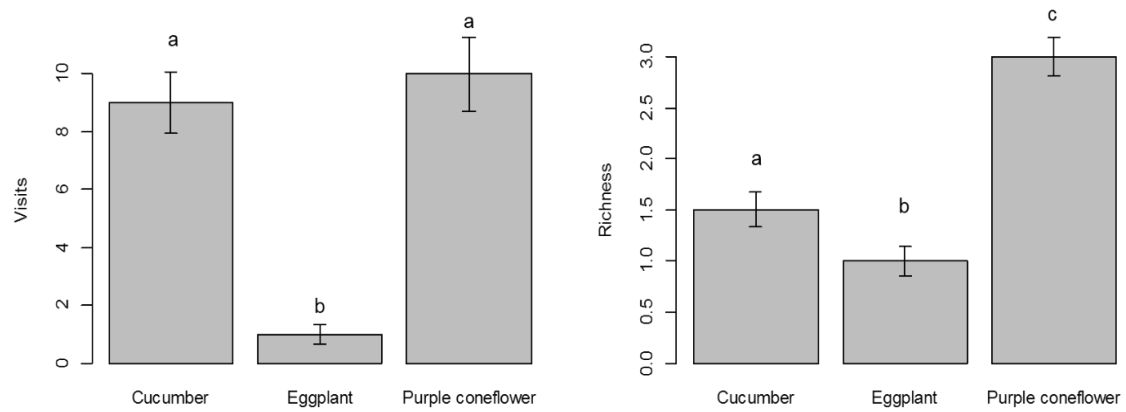


Figure 2. Median number of pollinator visits and pollinator taxonomic richness to each mobile garden plant species (+SE) across all trials. Letters indicate significant differences at  $P < 0.05$ .

## APPENDICES

Appendix 1. Residents' responses to survey about management practices in their yards. The survey was distributed to residents after the mobile garden had been removed from their yards.

Question on survey	Responses
How long have you resided at current residence?	16.3 + (SD) 11.6 years
Are the following features in your yard: Grass/Lawn Vegetable garden Weeds Flower garden* Flower pots	Y= 30, N=0 Y=17, N=13 Y = 14, N = 16 Y= 24, N =6 Y =19, N=11
Have you added or removed plants in the last year?	Y= 23, N=7
Have you applied insecticide this year?	Y=6, N=24
How many times per month do you mow your lawn?	2.4 + (SD) 1.2

\* A negative answer did not mean that a resident's yard had no flowers. Rather residents indicated that they did not intentionally plant a flower garden.

Appendix 2. Pearson's correlation coefficients (r) of pollination service metrics for each mobile garden plant species. Cucumber seed set was transformed prior to analysis by adding 1 and log-transforming the sum. Bolded values are significant at  $P < 0.05$ : \*:  $P \leq 0.05$ , \*\*:  $P < 0.01$ , \*\*\*:  $P < 0.001$

Pollination services metrics	Cucumber seed set	Eggplant fruit set	Eggplant seed set	Purple coneflower fruit set
Cucumber fruit set	<b>0.53***</b>	0.24	<b>0.39*</b>	<b>0.58***</b>
Cucumber seed set		0.02	<b>0.42*</b>	0.30
Eggplant fruit set			<b>0.45**</b>	0.33
Eggplant seed set				<b>0.35*</b>

Appendix 3. List of how many residential yards each flowering plant was recorded along with mean ( $\pm$ SE) floral abundance.

Plant	N yards	Mean floral abundance per yard	SE
<i>Achillea millefolium</i>	3	40.3	24.9
<i>Aegopodium podagraria</i>	1	77.0	0
<i>Agapanthus</i> spp.	1	1.0	0
<i>Agastache</i> spp.	3	16.3	5.9
<i>Ageratum</i> spp.	2	101.0	24.0
<i>Alcea rosea</i>	1	15.0	0
<i>Allium</i> spp.	4	3.5	1.1
<i>Alyssum</i> spp.	6	392.2	145.2
<i>Anethum graveolens</i>	6	33.2	12.4
<i>Antirrhinum</i> spp.	4	10.0	3.6
<i>Aquilegia</i> spp.	3	45.3	34.2
<i>Arctium lappa</i>	2	17.5	7.4
<i>Argyranthemum frutescens</i>	2	7.5	1.1
<i>Astilbe</i> spp.	1	100.0	0
<i>Barbarea verna</i>	1	20.0	0
<i>Begonia</i> spp.	6	149.2	101.8
<i>Borago officinalis</i>	1	61.0	0
<i>Brassica</i> spp.	3	29.3	18.4
<i>Brassica oleracea</i>	1	2.0	0
<i>Buddleja davidii</i>	3	34.3	9.4
<i>Calibrachoa</i> spp.	3	74.3	27.6
<i>Calystegia</i> spp.	1	18.0	0
<i>Campanula</i> spp.	3	19.0	5.0
<i>Capsicum</i> spp.	3	12.7	2.9
<i>Celosia</i> spp.	3	18.7	11.2
<i>Cerastium vulgatum</i>	1	4.0	0

<i>Chenopodium album</i>	1	8.0	0
<i>Clematis</i> spp.	7	61.7	17.4
<i>Cleome hassleriana</i>	1	18.0	0
<i>Commelina communis</i>	13	9.0	2.7
<i>Convolvulus</i> spp.	7	33.0	14.5
<i>Coreopsis</i> spp.	8	81.3	28.8
<i>Coriandrum sativum</i>	4	53.8	29.5
<i>Corydalis lutea</i>	1	195.0	0
<i>Cosmos bipinnatus</i>	1	10.0	0
<i>Cucumis sativus</i>	8	95.5	43.1
<i>Cucurbita pepo</i>	6	12.0	7.9
<i>Cyclamen persicum</i>	2	24.0	7.1
<i>Dahlia</i> spp.	2	5.0	2.8
<i>Daucus carota</i>	4	54.8	25.3
<i>Dianthus</i> spp.	6	78.2	62.4
<i>Digitalis</i> spp.	1	10.0	0
<i>Dodecatheon</i> spp.	1	2.0	0
<i>Echinacea purpurea</i>	6	73.7	36.5
<i>Erigeron strigosus</i>	6	67.5	34.3
<i>Fragaria</i> spp.	3	5.3	2.3
<i>Galinsoga ciliate</i>	6	566.2	311.9
<i>Geranium maculatum</i>	2	10.0	6.4
<i>Gladiolus</i> spp.	3	10.0	1.9
<i>Glechoma hederacea</i>	1	13.0	0
<i>Helianthus annuus</i>	3	6.0	2.4
<i>Hemerocallis</i> spp.	4	8.5	4.3
<i>Heuchera</i> spp.	2	30.5	18.7



<i>Hibiscus syriacus</i>	6	36.3	19.4
<i>Hosta</i> spp.	13	38.9	11.0
<i>Hoya carnosa</i>	1	14.0	0
<i>Hydrangea</i> spp.	10	123.8	45.8
<i>Hylotelephium</i>	1	3.0	0
<i>Impatiens</i> spp.	15	127.6	32.3
<i>Ipomoea purpurea</i>	7	18.6	9.5
<i>Iris</i> spp.	1	2.0	0
<i>Jasminum</i> spp.	1	3.0	0
<i>Lablab purpureus</i>	2	8.0	3.5
<i>Lactuca sativa</i>	1	59.0	0
<i>Lamium amplexicaule</i>	2	11.0	7.1
<i>Lamium maculatum</i>	1	25.0	0
<i>Lantana</i> spp.	2	6.0	0.7
<i>Lathyrus latifolius</i>	3	91.0	43.5
<i>Lavandula</i> spp.	4	200.8	84.6
<i>Lepidium</i> spp.	11	43.3	19.9
<i>Leucanthemum</i> spp.	5	56.2	23.1
<i>Liatris spicata</i>	4	6.3	1.7
<i>Ligustrum</i> spp.	1	44.0	0
<i>Lilium</i> spp.	13	21.8	6.6
<i>Linum usitatissimum</i>	1	51.0	0
<i>Lobelia erinus</i>	5	201.4	92.7
<i>Lonicera</i> spp.	1	43.0	0
<i>Lychnis coronaria</i>	1	58.0	0
<i>Malus</i> spp.	1	10.0	0
<i>Malva neglecta</i>	1	65.0	0
<i>Malva sylvestris</i>	1	52.0	0
<i>Melissa officinalis</i>	1	66.0	0
<i>Mentha</i> spp.	11	32.3	10.3
<i>Monarda</i> spp.	4	36.5	23.2

<i>Myosotis</i> spp.	3	8.0	2.6
<i>Nepeta cataria</i>	3	101.3	55.3
<i>Ocimum basilicum</i>	5	6.8	1.5
<i>Origanum</i> spp.	2	149.5	29.3
<i>Oxalis</i> spp.	23	35.6	9.3
<i>Pelargonium</i> spp.	14	17.9	7.7
<i>Penstemon</i> spp.	1	68.0	0
<i>Perovskia atriplicifolia</i>	2	840.0	569.9
<i>Petroselinum crispum</i>	1	14.0	0
<i>Petunia</i> spp.	11	123.7	64.2
<i>Phlox</i> spp.	9	51.4	23.3
<i>Physalis</i> spp.	1	50.0	0
<i>Physalis philadelphica</i>	1	9.0	0
<i>Phytolacca</i> spp.	1	35.0	0
<i>Plantago lanceolata</i>	3	15.7	5.3
<i>Plantago major</i>	9	58.6	24.2
<i>Platycodon grandiflorus</i>	2	17.5	7.4
<i>Polygonum</i> spp.	10	36.6	9.9
<i>Portulaca</i> spp.	4	10.0	3.2
<i>Ranunculus</i> spp.	2	36.5	19.4
<i>Ratibida</i> spp.	1	197.0	0
<i>Rhododendron</i> spp.	1	57.0	0
<i>Rondeletia leucophylla</i>	1	23.0	0
<i>Rosa</i> spp.	23	140.0	55.0
<i>Rubus</i> spp.	1	31.0	0
<i>Rudbeckia</i> spp.	8	128.6	84.4
<i>Salvia</i> spp.	7	117.5	54.8
<i>Salvia azurea</i>	3	51.3	22.5
<i>Salvia splendens</i>	4	38.0	21.1
<i>Saponaria officinalis</i>	2	78.5	11.0

<i>Scabiosa japonica</i>	2	34.5	15.9
<i>Sedum acre</i>	4	179.0	74.4
<i>Silene</i> spp.	1	19.0	0
<i>Solanum dulcamara</i>	12	16.3	3.5
<i>Solanum lycopersicum</i>	15	44.8	10.8
<i>Solanum melongena</i>	1	8.0	0
<i>Solanum ptycanthum</i>	4	22.5	14.4
<i>Solanum tuberosum</i>	1	11.0	0
<i>Sonchus oleraceus</i>	15	6.1	1.8
<i>Spiraea</i> spp.	3	120.3	24.1
<i>Stachys</i> spp.	1	12.0	0
<i>Stellaria nemorum</i>	2	2.0	0
<i>Stokesia laevis</i>	1	5.0	0
<i>Sutera cordata</i>	1	17.0	0
<i>Syringa</i> spp.	2	73.0	48.1
<i>Tagetes</i> spp.	12	51.7	15.7
<i>Tanacetum parthenium</i>	1	54.0	0
<i>Taraxacum officinale</i>	14	6.0	1.4
<i>Thymus vulgaris</i>	7	167.6	90.6
<i>Torenia fournieri</i>	1	79.0	0
<i>Tradescantia</i> spp.	4	57.3	43.3
<i>Trifolium pratense</i>	3	5.3	0.3
<i>Trifolium repens</i>	17	648.7	200.7
<i>Triodanis perfoliata</i>	2	2.5	0.4
Unidentified	15	90.7	32.2

<i>Verbascum thapsus</i>	1	2.0	0
<i>Verbena</i> spp.	6	22.5	8.1
<i>Veronica</i> spp.	1	12.0	0
<i>Veronicastrum</i> <i>virginicum</i>	1	26.0	0
<i>Viburnum</i> spp.	4	42.8	25.3
<i>Vinca minor</i>	5	55.8	24.3
<i>Viola</i> spp.	5	225.6	116.7
<i>Weigela</i> spp.	3	95.0	47.1
<i>Zantedeschia</i> <i>aethiopica</i>	3	3.0	1.3
<i>Zinnia elegans</i>	2	15.0	0.7

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## **Chapter II. Diversity in flowering plants and their characteristics: Integrating humans as a driver of urban floral resources**

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### **Abstract**

Urban neighborhoods vary in development intensity and in the life style and demographics of their residents. Decisions made by urban residents affect plant communities, their functional characteristics, and the floral resources they provide. We recorded flowers in front-facing yards in 58 neighborhoods in Chicago, IL (USA) and examined patterns in community composition and species turnover between neighborhoods. We investigated how species richness and plant traits, including origin, cultivation intent, and life cycle, are affected by neighborhood socioeconomic factors. Urban plant species tended to be perennial, ornamental, and non-native. White clover had the broadest distribution and the highest floral abundance but was not present in several of the highest-income neighborhoods. Although we found 144 morpho-species across neighborhoods, most occurred infrequently. Species turnover was highest for ornamental species and lowest for weedy species, suggesting that intentional plantings are driving beta diversity across the landscape. We found the highest species richness in neighborhoods with intermediate numbers of Hispanic and white residents and with intermediate number of residential lots; neighborhoods with racially or ethnically homogenous populations had fewer plant species. The high frequency of weeds in low-income neighborhoods, the occurrence of certain ornamental plant species in whiter, wealthier communities, and high turnover of species from one neighborhood to another, all suggest a disparity in plant-related ecosystem services across cities.

Complexity in urban plantings may be influenced by the suite of perspectives that residents bring towards habitat management. Cultivation sustains a diversity of plants and creates a disparity in plant traits by neighborhood socioeconomics.

## **Introduction**

As the percentage of global population residing in cities continues to increase, there is a need for healthy and sustainable urban areas. Urban ecosystems potentially provide many important resources to residents. For example, local plants deliver a number of economic and social benefits, including fresh produce, aesthetics (Goddard et al. 2013), and connection to nature (Fuller et al. 2007, Luck et al. 2011). However, the fine-scale heterogeneity of cities (Cadenasso et al. 2007), and the patchwork of small, private parcels of land, creates patchy plant communities that may not provide benefits equally across a city.

Residential yards play an important role in urban plant biodiversity (Gaston et al. 2005, Bertoncini et al. 2012, Knapp et al. 2012). Making up between 25-47% of urban green space (Loram et al. 2007, Mathieu et al. 2007), yards reflect a managed ecosystem that contributes to plant, invertebrate, and bird diversity (Loram et al. 2007, Lerman and Warren 2011, Belaire, et al. 2014). Front yards are diverse and can include food gardens, flower gardens, and turf grass. Some yards are actively managed for wildlife (Goddard et al. 2013), and many are tended carefully for cultural or social purposes (Grove et al. 2006). Rather than soil type or other environmental characteristics, behavioral decisions of urban residents have a strong effect on urban vegetation. Humans further influence yard vegetation by modifying canopy cover, adding nutrients and water, and using herbicides. As a result, many yards are dominated by non-native, cultivated plants sourced from garden centers (Pysek 1998, Cook et al. 2012, Aronson et al. 2015). Since many of these plants are flowering species, the decision of what to plant or remove

has profound consequences for animals that use floral resources.

As a managed ecosystem, urban vegetation cover and diversity are influenced by demographic and socioeconomic factors. Income (Hope et al. 2003, Mennis 2006), ethnicity (Minor et al. in press), family life stage and education (Grove et al. 2006), housing age (Smith et al. 2005), human population density (Lowenstein et al. 2014), and housing density (Knapp et al. 2012) are associated with plant community patterns in residential yards. Although cities have been drastically altered from their natural habitats, environmental pressures such as nighttime lighting and altered soil chemistry still select for and against plants (Williams et al. 2009). Human behavior may act independently or concurrently with abiotic drivers to influence plant traits in yards (Kendal et al. 2012, Goddard et al. 2013). Many questions remain about how humans influence plant traits. A meta-analysis suggested that urbanization may favor taller species with larger seeds, although this trend did not hold true for all cities (Duncan et al. 2011). Other studies conflict on whether native (La Sorte et al. 2014, Bertoncini et al. 2012) or non-native flora (Knapp et al. 2012, Aronson et al. 2015) are dominant in cities. It is not known how traits such as life cycle (e.g., annual vs. perennial) or native status may change between different neighborhoods within a city.

A recent editorial (Hahs and Evans 2015) called for more research on functional ecology in urban ecosystems. Here, we respond to that call by examining plant attributes and functional traits, distribution, and composition of floral resources in residential, front-facing yards in a highly developed U.S. city. By surveying flowering plants across neighborhoods of different socioeconomic status, we aim to understand how plant traits vary at a fine scale within urban areas. We classify plants according to their life cycle (annual versus perennial), region of origin (native versus non-native), and intent of cultivation (ornamental versus weedy), and ask how

income, race, and other socioeconomic factors affect floral resources with respect to these traits. We identify drivers of 1) plant species richness, 2) community composition, 3) turnover, and 4) several functional traits in urban neighborhoods. As flowering plants provide important resources for numerous animal species, our work contributes to an understanding of how humans affect biotic interactions and ecosystem function.

## **Methods**

We recorded all open flowers on herbaceous plants and shrubs on 58 urban residential neighborhood blocks (called “neighborhoods” from here forward) in and around Chicago, Illinois (see map of study sites in Figure S1). Site selection was non-random to include neighborhoods across a gradient of socioeconomic conditions (Table 1), enabling a comprehensive assessment of urban floral community composition. Neighborhoods included multi-story apartment dwellings, single family homes, and multi-family two- or three-flats.

We visited each neighborhood twice in summer 2013: a first time between 10 June and 19 July, and a second time approximately 25-30 days later between 25 July and 21 August. Consequently, our methods do not account for plants that bloom during the spring or fall months. We recorded both taxonomic richness of flowers and floral abundance along a 150 m transect that centered on the sidewalk. We counted flowers in a 5 m buffer on either side of the transect and identified flowers to the species level when possible, or to genus level if species identification was not possible (e.g. for genera with many hybrid varieties). We refer to all identified plants, including those identified only to the genus level, as ‘species’ from here forward. To quantify floral abundance, we counted the number of floral units for each species. A floral unit consisted of a raceme, umbel, spike, capitulum, or a single flower, depending on the morphology of the plant (see Baldock et al. 2015, Lowenstein et al. 2015). We pooled flower



abundance and species presence at each neighborhood over both sample dates for all analyses.

### *Classifying plants*

All recorded plants were classified by three traits. First we categorized plants by their life cycle in USDA Plant Hardiness Zone 6A, corresponding to Chicago, IL, as surviving for multiple years (biennial or perennial) or surviving for a single year (annual). Second, we classified plants as native or non-native, defining ‘native’ as plants that evolved in the area east of the Rocky Mountains of the United States. We used taxonomic guides and the Missouri Botanical Garden plant finder when characterizing plant life cycle and origin. Finally, we classified plants by their intent of cultivation as ornamental or weedy species. A plant was classified as ornamental if available for purchase in a garden center or nursery and usually planted intentionally. Weedy plants included species such as *Trifolium repens* L. (white clover) and *Taraxacum officinale* F.H. Wigg (dandelion) that tend to be regularly mowed by homeowners or removed by landscaping companies and also included species that are listed as weedy by turfgrass companies. In a small number of cases, we could not easily classify a plant into one group or another; these species were excluded from the relevant analyses and are noted in Table S1.

### *Socioeconomic variables*

To assess the impact of socioeconomic factors on floral communities, we measured several socioeconomic variables from each neighborhood, using block group data from the U.S. Census 5 year American Community Survey 2008-2012. These variables, which were selected based on prior studies of neighborhoods in Chicago (Minor et al. in press) and other cities (e.g., Grove et al. 2006, Knapp et al. 2012, Goddard et al. 2013), included percentage of renter-occupied households, percentage of residents identifying as Hispanic, percentage of residents

identifying as white, human population density, and median household income (Table 1). The percent of residents identifying as black or African-American was not included, as this variable is highly correlated with income and with the percent of residents identifying as white.

Additionally, we summed the total number of residential lots per neighborhood as a measure of development density. Two sets of socioeconomic variables were significantly correlated: percent renter occupied and income ( $r = -0.52$ ,  $P < 0.01$ ) and percent white and income ( $r = 0.59$ ,  $P < 0.001$ ).

#### *Data analysis - univariate*

We used independent t-tests to test for dominance in terms of life cycle, origin, and cultivation intent of plants. We also calculated species rank and abundance in two different ways to compare frequency of plant species in neighborhoods. First, we calculated rank and abundance based on geographic distribution, by counting the number of neighborhoods in which each species was observed. Second, we calculated rank and abundance based on the total floral abundance of each species over all neighborhoods.

We also investigated whether overall taxonomic richness, or richness of different plant groups (native, non-native, perennial, annual, weedy, ornamental), was influenced by neighborhood socioeconomic characteristics through best subsets regressions. We focused our modelling analyses on richness, as this type of presence/absence data is less prone to bias than our measure of floral abundance. We further divided ornamental plants into annual and perennial plants, as ornamental annuals may indicate greater resource allocation towards residential gardens. Species richness data met the assumptions of normality.

We used a model selection approach with multiple regression to test the effect of predictor variables on species richness. Upon inspecting model diagnostics, we identified several

non-linear (quadratic) relationships between predictor variables and response variables. If a lower-order predictor variable selected in the model selection procedure was determined to have a non-linear relationship with the response variable, we also included the quadratic predictor term in model selection. We compared the final best performing models, as identified by best subsets regression, using  $\Delta AICc$ . We examined the relative importance of each variable in explaining species richness by calculating the Akaike weight for each predictor variable. All modeling was performed using the leaps library in R 3.1 (Lumley 2009).

### *Multivariate analyses*

To quantify change in the plant community from one neighborhood to another, we calculated two measures of beta diversity for each plant group. The first, “true beta diversity” (Whittaker 1960, Tuomisto 2010), was calculated by dividing the total number of species over all sites (i.e., gamma diversity) by the average number of species at a single site (i.e., alpha diversity). The second, Sorenson index, corrects for the increase in turnover as more sites are included through incorporating a pairwise comparison of the sites with the formula

$$Beta = (b + c) / (2a + b + c)$$

where  $a$  is the number of shared species in two sites, and  $b$  and  $c$  represent the number of species unique to each site. This index was averaged over all pairs of sites.

We used Nonmetric Multidimensional Scaling (NMDS) with Bray-Curtis distance to visualize patterns of association among plant species in different groups and used the final stress value of the ordination to evaluate the fit. We then overlaid the socioeconomic variables that were significantly ( $P < 0.05$ ) correlated with plant community composition. Prior to analysis, we Hellinger-transformed the plant community matrices to reduce the weight of rarer species. All plants that could not be identified to genus as well as those appearing on only a single block

(totaling 5% of all plants) were excluded from community matrices. We used the vegan package in R 3.1 for all multivariate procedures.

## Results

### *Plant characteristics*

In total, we identified 120 plant species and an additional 24 genera for which we could not distinguish among species (Table S1). When considering all species recorded over all neighborhoods, 104 species were ornamental (72% of classified species), 96 were perennial (69% of classified species), and 104 were non-native (76% of classified species). On average, each neighborhood contained 28 ( $\pm 1.2$  SE) flowering species and 3407 ( $\pm 394$  SE) floral units. The t-tests indicated that, at the neighborhood scale, most species were ornamental ( $t=7.25$ ,  $P<0.01$ ), perennial ( $t=9.49$ ,  $P<0.01$ ), and non-native to the region ( $t=17.54$ ,  $P<0.01$ ; Fig. 1). Similarly, at the neighborhood scale, perennial ( $t=5.31$ ,  $P<0.01$ ) and non-native ( $t=10.4$ ,  $P<0.01$ ) floral units were most abundant. The floral abundance of weedy and ornamental plants did not significantly differ ( $t=0.64$ ,  $P=0.52$ ).

On average, each species was observed in 11.6 neighborhoods. However, rank abundance diagrams indicated an uneven community, with a relatively small number of common species in terms of floral abundance and geographic distribution (Figs. 2, S2). Only 15% ( $N = 21$ ) of species were present in  $> 50\%$  of neighborhoods, while nearly half were recorded in five or fewer neighborhoods. This disparity is magnified when considering floral abundance. *Trifolium repens*, the most abundant plant in terms of both geographic distribution and floral abundance, had more than twice the number of floral units than the second most abundant plant. Other common plants included *Plantago major* L., *Impatiens* spp., *Petunia* spp., and *Rosa* spp.

### *Best subsets regression for species richness*

We identified a moderate to strong effect of socioeconomic variables ( $0.40 > R^2 > 0.52$ ) on richness of all plant groups except for native plants. We detected non-linear relationships between socioeconomic variables and total species richness, as well as richness of five other plant traits (Table 2). Total species richness was best explained by a nonlinear effect of number of residential lots, percent white residents, and percent Hispanic residents (Fig. 3). With the exception of weedy plants and annuals, richness of all plant groups showed a nonlinear relationship with number of residential lots, peaking at an intermediate development level. Weedy plant richness was unrelated to the number of lots, while annual plant richness was linearly and positively related. Other important predictor variables included the percent of white residents (selected for 6 plant groups), and percent of Hispanic residents (selected for 6 plant groups). Income appeared in one model, showing a significant negative linear relationship with weedy species richness (Fig. 4). Model selection identified several ‘best’ models with  $\Delta AIC_c < 2$  for total species richness, weedy, native, and annual ornamental plants.

#### *Beta diversity*

Ornamental annual species had the greatest beta diversity, while weedy species had the lowest beta diversity (Table 3). Sorenson indices tended to be in agreement with beta diversity, suggesting an intermediate degree of turnover of all plant species between sites and the greatest turnover in ornamental plant species.

#### *Multivariate analyses*

A 3-dimensional NMDS ordination for total plant community composition shows an apparent geographic separation of weedy and ornamental plants along three axes (stress = 0.16; Fig. 5). All weedy plants are on the left side of the horizontal axis (NMDS1); a few species of interest are labeled. Household income ( $r=0.73$ ,  $P<0.01$ ), the percent of white residents ( $r=0.62$ ,

$P < 0.01$ ), percent renter occupied households ( $r = 0.44$ ,  $P < 0.01$ ), and human population density ( $r = 0.36$ ,  $P = 0.03$ ) were related to plant community composition.

## **Discussion**

Flowers in Chicago neighborhoods are predominantly on ornamental, non-native and perennial plants. Our results provide further evidence that non-native plants are common in densely populated regions (Pysek 1998, Clemants and Moore 2001, Cook et al. 2012, Aronson et al. 2015) and particularly in yards, where they can comprise >50% of total species in some cities (Smith et al. 2006, Knapp et al. 2012; but see Bertoncini et al. 2012). While Chicago residents appear unconcerned about the origin of their ornamental plants, the trend to cultivate perennial plants, which have reduced yearly planting costs, was nearly identical in British gardens (Smith et al. 2006).

Floral resources were not uniform across neighborhoods. Rank abundance diagrams revealed that >50% of species appeared in fewer than half of neighborhoods, and that these infrequently occurring species had 12x fewer floral units than more common plants. Some ornamental plants can escape from cultivation to unmanaged spaces (Reichard and White 2001, Dehnen-Schmutz et al. 2008), further contributing to a plant community dominated by several commonly occurring and many infrequently appearing species. Both spontaneously-growing weeds and cultivated ornamentals were among the most common species. However, beta diversity was lower for weeds than for ornamental species, indicating that the same weeds are found almost everywhere and that human choices may be most responsible for large-scale (i.e., gamma) diversity across the city. On the other hand, beta diversity of weeds could have been higher if less-managed areas such as industrial areas or railroad rights-of-way were included in sampling.

Cultural preferences in ethnically diverse neighborhoods likely influence the characteristics of yard plantings and contribute to the high turnover in ornamental plants from one neighborhood to another. We observed that neighborhoods with intermediate percentages of Hispanic and white residents had greater species richness across multiple plant traits. The unimodal relationship suggests that yard management and/or preferences differ across ethnic and racial groups in Chicago neighborhoods. Other research indicates that ornamental flowers in pots or raised beds (Kent 1999) as well as floral density and vegetation other than herbaceous plants are greater in majority Hispanic areas (Taylor and Lovell 2015, Minor et al. in press). Compared to low and middle income white and African-American households, Hispanic residents' greater participation in outdoor water-gardening (Dennis and Behe 2007) and in food gardening in multifamily lots (Taylor and Lovell 2015) may also play a role. Residential yards offer an outlet for social and cultural expression that can lead to a greater diversity of plants in neighborhoods without a dominant ethnic or racial majority.

With the exception of weedy species, richness across all traits was significantly related to number of residential lots. Most plant groups showed a non-linear relationship with number of lots, peaking in richness at intermediate-levels of development. The exception was annual species richness, which increased linearly with number of lots. However, several studies offer conflicting findings for positive (Knapp et al. 2012) and negative effects (Godefroid and Koedam 2007, Matteson et al. 2013) of building or development density on species richness. We offer four explanations for this discrepancy and for our novel finding of a peak in species richness at intermediate densities. First, the unit for measuring development is not standardized between studies. Building density, human population density, and number of lots all capture different aspects of the urban environment. Second, though linear relationships are documented for

socioeconomic drivers of plants (Hope et al. 2003, Knapp et al. 2012, Grove et al. 2014), non-linear relationships may not have been explored due to an interest in obtaining a parsimonious result. In our study, linear relationships between number of lots and species richness were also significant although had less explanatory power than non-linear relationships. Third, other studies may not have spanned the density or socioeconomic gradient to the same extent that our study did. Finally, in a previous study (Lowenstein et al. 2014), we speculated that richness of flowering plants might be highest in urban neighborhoods with moderately high human population density. We hypothesized that people have diverse preferences for plants, which creates more diverse plant communities in neighborhoods with more people. However, taken to the extreme of very densely populated neighborhoods with many homes, the amount of non-impervious surface decreases and shade increases (Matteson and Langellotto 2010), reducing residents' ability to plant as many species as they might want to. The linear increase we observed here for annual species might be explained by flowers in small 'pot gardens' on porches and patios. This last argument is further supported by the fact that weedy species richness was not related to number of lots (i.e., weedy species richness is not driven by diverse human preferences).

The ordination of plant species suggests that income and race—but not number of residential lots—are linked with plant community composition. By symbolizing species according to their ornamental or weedy status, we confirmed that wealthier and whiter neighborhoods have fewer weeds. Weeds colonize rapidly, eventually reaching an equilibrium in species richness, in neighborhoods with unoccupied lots (Crowe 1979). Higher occupancy of lots as well as management in wealthier neighborhoods leads to their near absence, or complete absence in some cases, at sites with high median income. Another subset of plant species, including *Allium*



*spp.*, *Nepeta cataria* L., *Perovskia atriplicifolia* Benth., Begonia, and Hydrangea, are also closely linked with these neighborhoods. We hypothesize that this particular set of ornamental plants may be attributed to the commercial landscaping companies we observed working in high-income neighborhoods. These plants may be recommended by the landscaping companies or, alternatively, may simply reflect the status or desired status of neighborhood residents (Grove et al. 2006).

#### *Effects of urban floral patterns on higher trophic levels*

The dominance of non-native, cultivated and weedy species in certain neighborhoods has implications for nectarivorous insects and birds. In cities, weeds are a useful, if undervalued, pollinator resource (MacIvor et al. 2013, Larson et al. 2014). While we observed more ornamental species than weedy species overall, there was no difference in floral abundance of ornamental and weedy plants. Common cultivated species with higher floral abundance in urban neighborhoods tend to produce little pollen and or low-quality nectar (Comba et al. 1999). These included species such as Petunia and Impatiens, which were present on most neighborhood blocks, but are visited by few pollinators (DML unpublished). However, other ornamental species found in approximately 1/3<sup>rd</sup> of Chicago neighborhoods, including *Hibiscus syriacus*, *Leucanthemum* and *Coreopsis*, have attractive floral stalks to pollinators, unique floral morphology, and long blooming periods. Furthermore, plants vary in attractiveness to insects within cultivars (Garbuzov and Ratnieks 2014).

Our finding of high turnover in plants suggests that while community composition varies between neighborhoods, there remains a diversity of nectar-rich plants with multiple traits. The co-occurrence of non-native and native plants enriches overall urban plant diversity and likely extends the flowering season, even though individual non-native species are often recorded at

low frequencies (Cook et al. 2012). This diversity makes cities more beneficial than expected for pollinators (Leong et al. 2014, Lowenstein et al. 2015). However, it can come at the expense of phylogenetic diversity (Knapp et al. 2012) and could reduce the taxonomic diversity of plants to only a few common families.

### *Conclusion*

We observed changing floral communities along an urban socioeconomic gradient. While most plants in our study area were perennial, non-native, and ornamental, species composition varied across the city and was driven predominantly by income and race. Species richness was a function of number of residential lots and percent of white and Hispanic residents. We should emphasize that our measured socioeconomic factors are only a proxy for the multi-scalar drivers that affect residents' decisions about their yards (Cook et al. 2012). Future interdisciplinary work is needed to understand these drivers and make cities more livable and supportive for a diversity of plants and animals. Large-scale efforts to change planting habits across a city are a long-term goal. In the shorter term, collaboration with breeders to diversify the morphology of common cultivars could supplement efforts to encourage residents to increase plant biodiversity. Our previous work in the Chicago area (Belaire et al. 2014, Lowenstein et al. 2015) already indicates the success of its residents at providing resources for many birds and invertebrates.

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## TABLES

Table 1. Summary statistics of socioeconomic variables as measured at the block group encompassing each study neighborhood (n = 58).

Variable (Unit)	Mean	SD	Range
Human population density (persons/km <sup>2</sup> )	17,930	1,256	4,594 – 39,583
Median household income (USD)	56,024	3,914	11,029-138,188
Renter occupied (%)	50	2	12-78
Hispanic residents (%)	24	4	0-95
White residents (%)	47	4	0-100
Number of residential lots	11	4	3-18

Table 2. Multiple regression models for effect of socioeconomic variables on plant species richness. Only variables included in models with  $\Delta\text{AICc} < 2$  are displayed. For each response variable, we show the direction of the coefficient (+ or -) and the variable importance, calculated by summing Akaike weights for the models in which the variable was included. A weight of 1 indicates this variable was included in all models with  $\Delta\text{AICc} < 2$ . We show  $R^2$  for the model with lowest AICc. \* indicates  $P < 0.05$ , \*\* indicates  $P < 0.01$

Plant group	SOCIOECONOMIC PREDICTOR VARIABLES								# models AICc < 2	$R^2$
	# lots	(# lots) <sup>2</sup>	% white	(% white) <sup>2</sup>	% Hispanic	(% Hispanic) <sup>2</sup>	Pop. Density	Income		
All plants	(+) 1	(-) 1	(+) 0.41	(-) 0.41	(+) 0.59	(-) 0.59			2	0.46**
Ornamental	(+) 1	(-) 1	(+) 1	(-) 1					1	0.50**
Weedy			(-) 0.37		(+) 0.18		(-) 0.13	(-) 1	4	0.43**
Perennial	(+) 1	(-) 1			(+) 1	(-) 1			1	0.40**
Annual	(+) 1				(+) 1				1	0.40**
Native	(+) 1	(-) 1	(+) 0.18	(-) 0.18	(+) 0.29	(-) 0.29			2	0.20*
Non-native	(+) 1	(-) 1			(+) 1	(-) 1			1	0.51**
Annual										0.52**
ornamental	(+) 0.77	(-) 0.55	(+) 1	(-) 0.55					2	
Perennial										0.40**
ornamental	(+) 1	(-) 1	(+) 1	(-) 1					1	



Table 3. Beta diversity values for plant characteristics. Beta diversity was calculated as total number of species recorded across all sites divided by the average richness per single site.

Sorenson index uses of pairwise comparison of sites and accounts for number of shared genera between sites, with values ranging from all shared genera (0) to no shared genera (1).

Characteristic	Beta diversity	Sorenson index
All	4.04	0.573
Ornamental	4.38	0.605
Weedy	3.00	0.503
Native	4.33	0.578
Non-native	3.84	0.539
Perennial	4.09	0.558
Annual	3.53	0.536
Ornamental perennial	4.14	0.591
Ornamental annual	4.53	0.517

## FIGURES

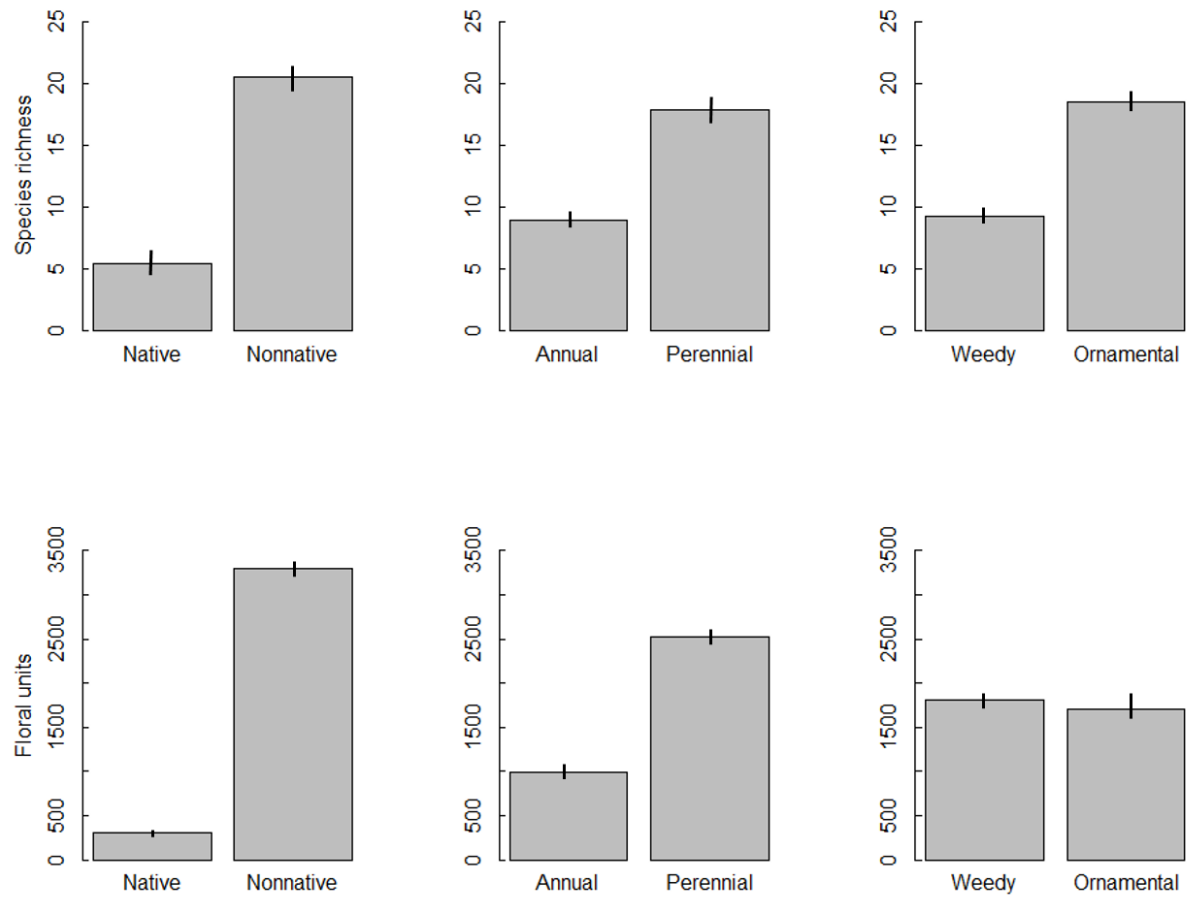


Figure 1. Mean ( $\pm$ SE) species richness and floral units of plant traits per neighborhood.

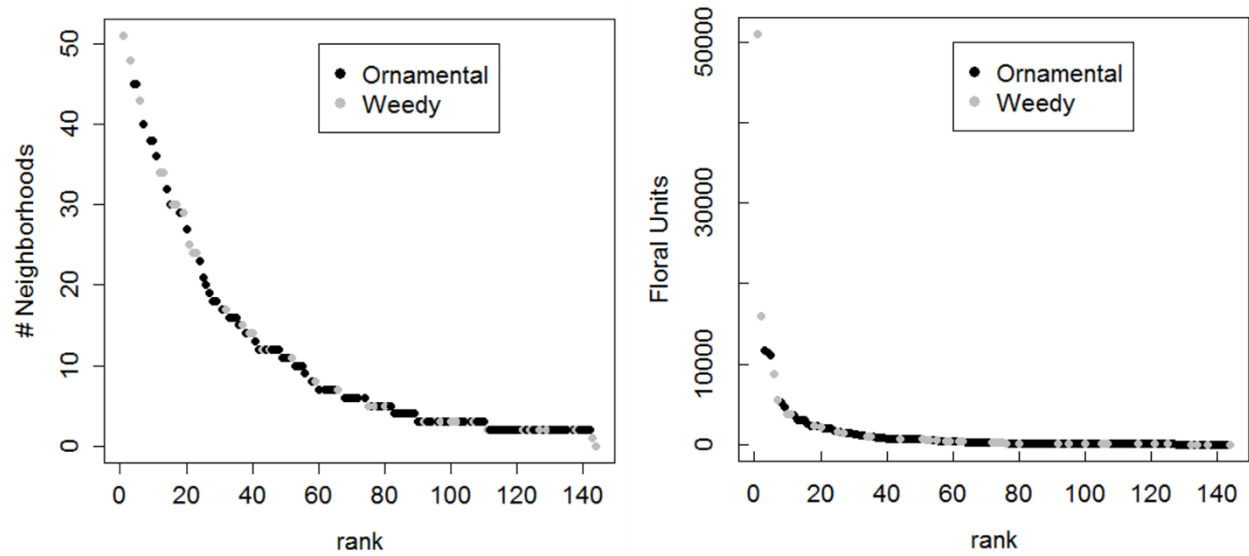


Figure 2. Rank abundance diagrams for geographic distribution (left) and floral abundance (right), classified according to cultivation intent. Rank abundance diagrams for other plant attributes are presented in Supplementary Material.

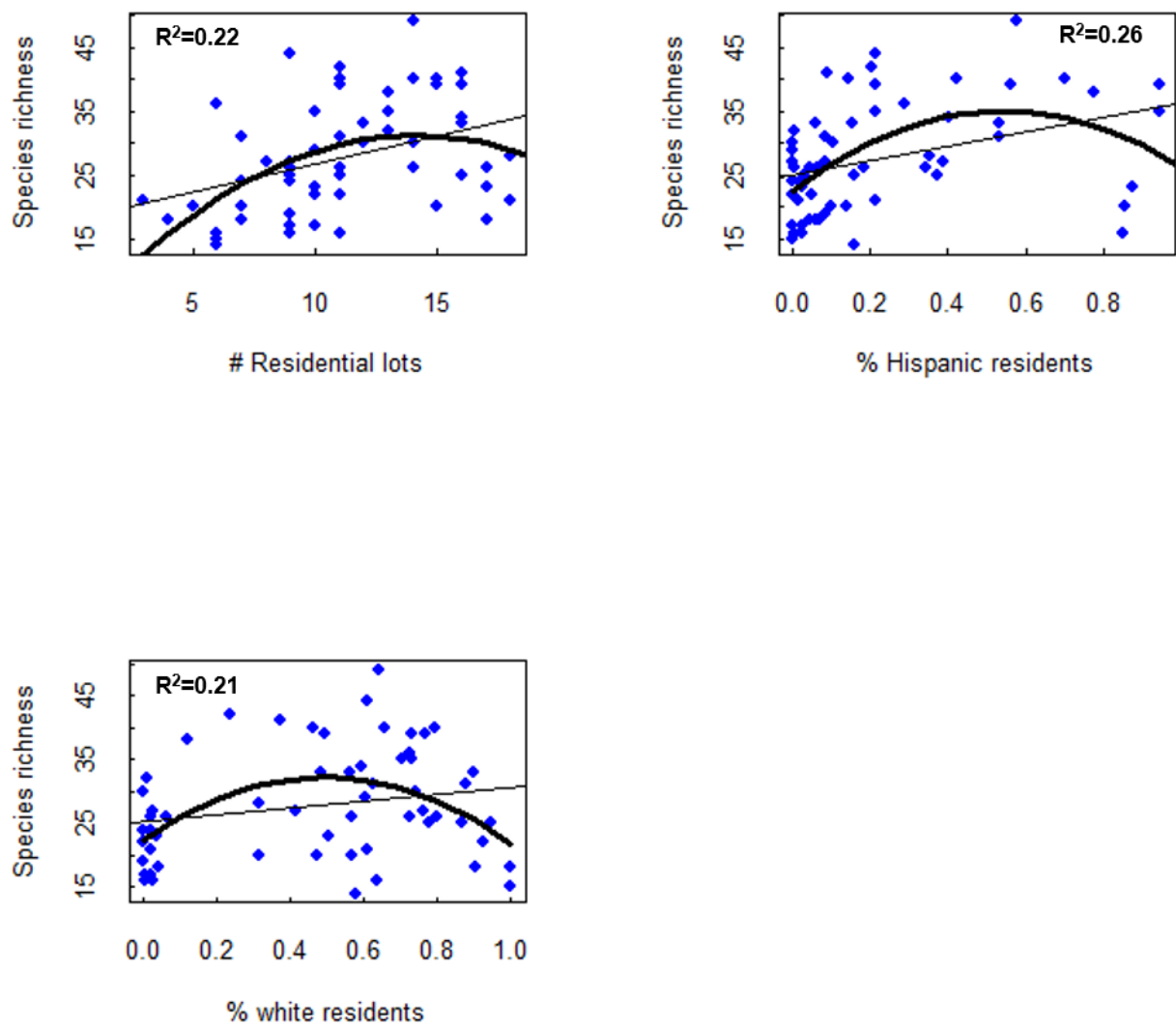


Figure 3. Fitted models for quadratic regression (bolded line) and linear regression (lighter line) for significant socioeconomic predictors of species richness for all plants.

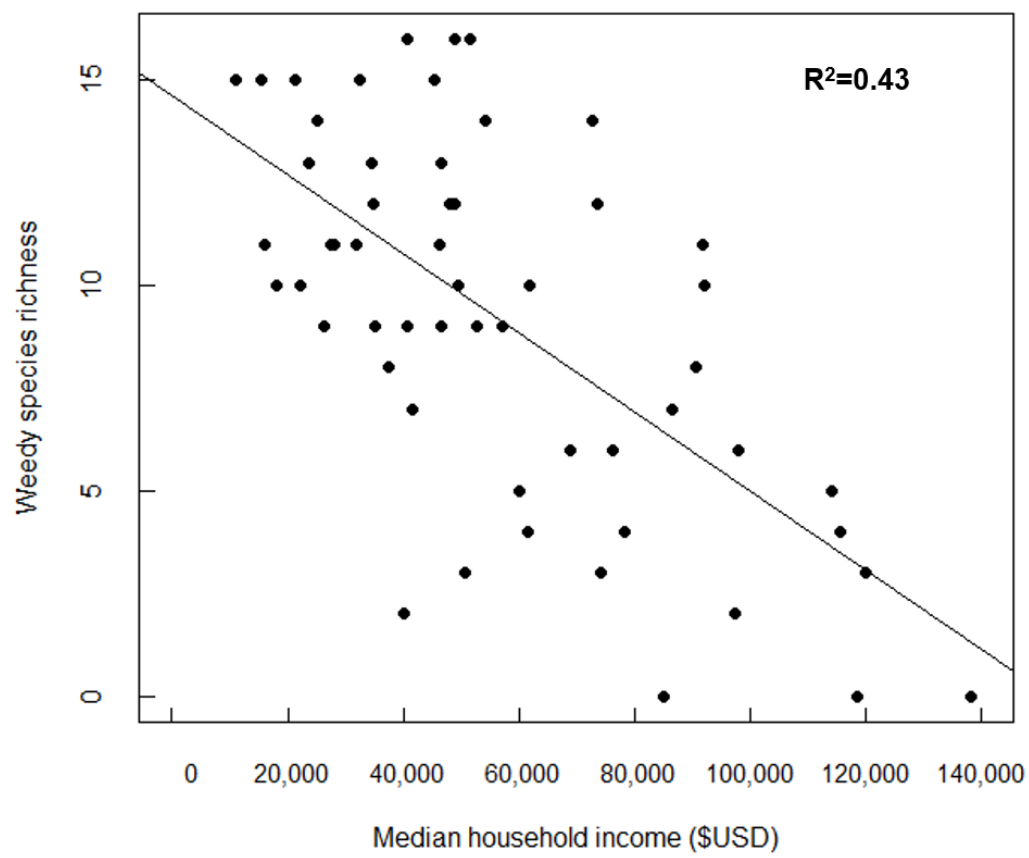


Figure 4. Fitted slope of median household income (USD) and weedy species richness indicating significant negative relationship

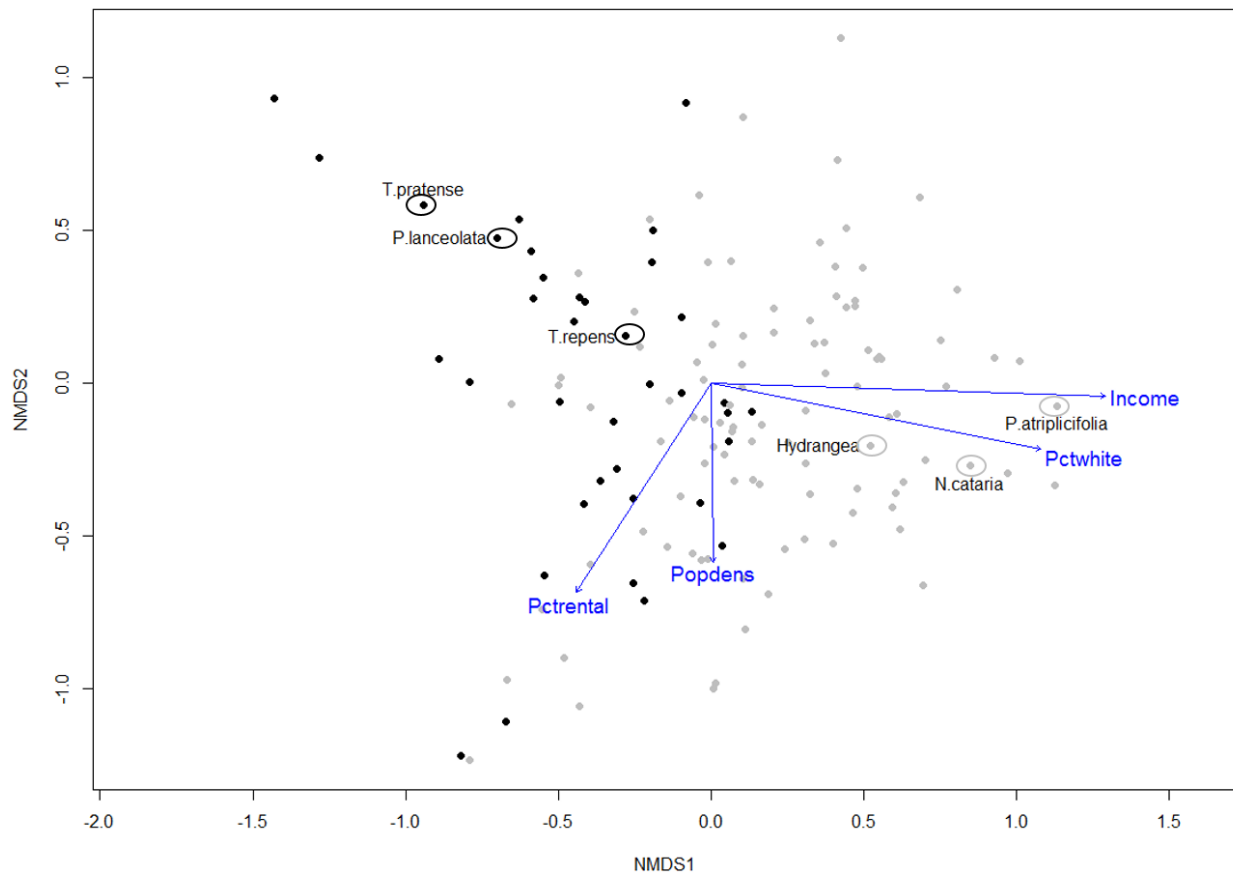


Figure 5. NMDS ordination of all species with ornamental plants shown in gray and weedy plants shown in black. The ordination had a 3-dimensional solution but the two axes that explain the greatest amount of variation are shown. Socioeconomic variables that significantly ( $P < 0.05$ ) explain community composition are overlaid as blue lines. Several common plant species are labeled.

## APPENDICES

Figure S1. Map of neighborhoods sampled in this study. Chicago is shown with a solid gray polygon; the hatched area indicates the central business district (i.e., downtown).

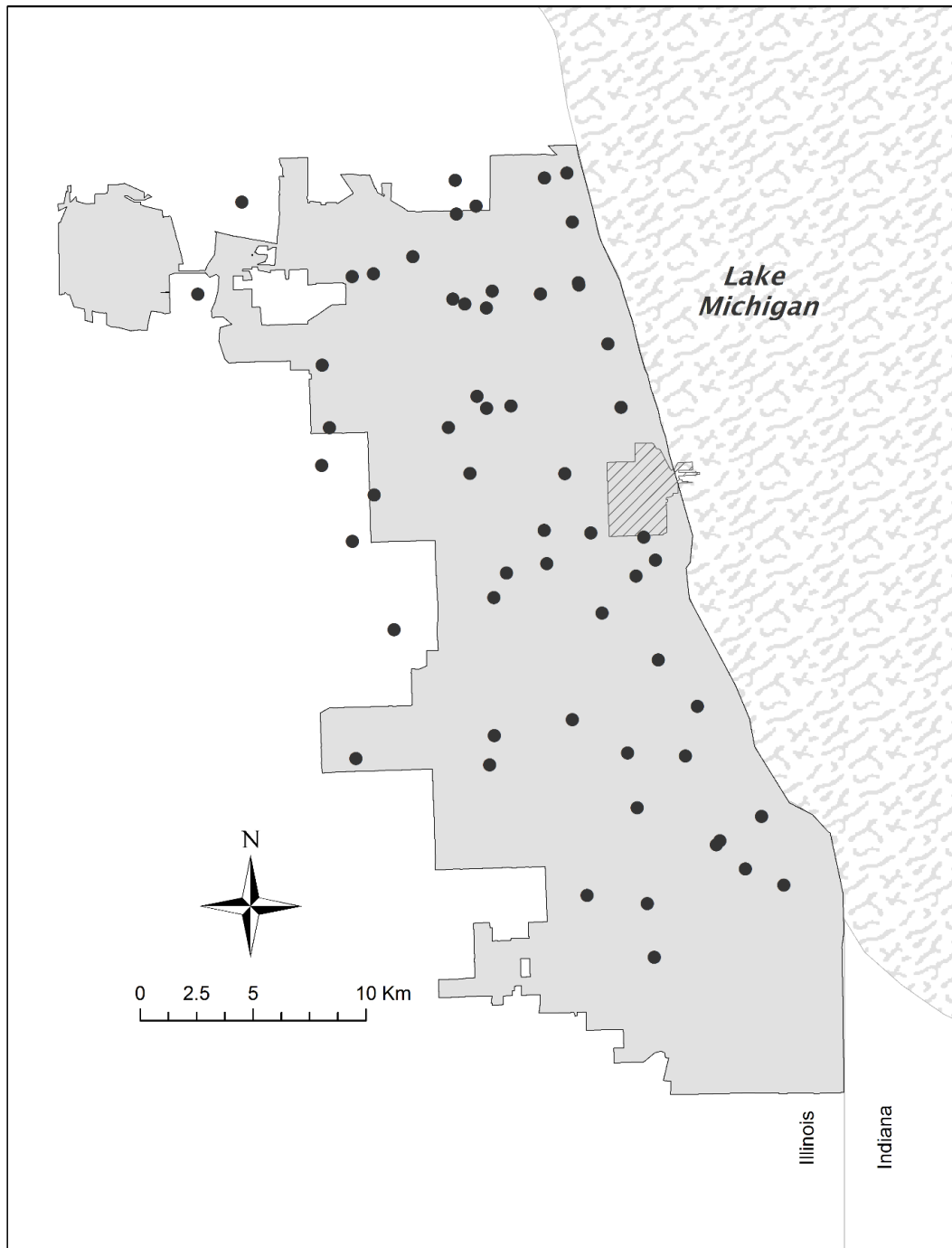


Figure S2. Rank abundance diagrams for geographic distribution (top row) and floral abundance (bottom row), with plants classified by origin and life cycle.

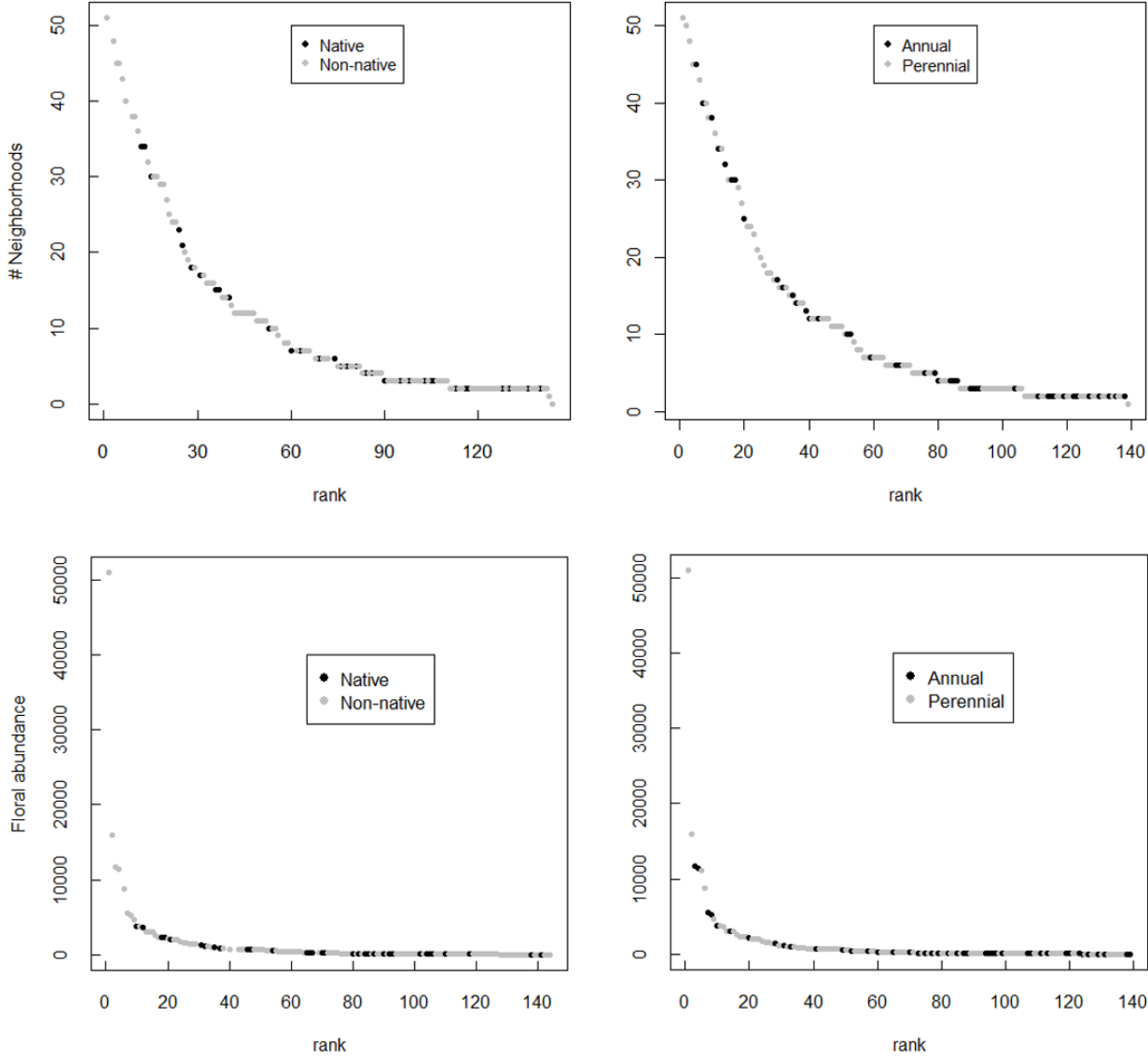




Table S1. List of plant species recorded on neighborhood blocks and their functional characteristics. Blank cells indicate that we were unable to make an objective classification for the following reasons: A) Plant grows as annual or perennial, B) Information unknown since the variety is a hybrid or the field identification was not to species level.

<b>Plant</b>	<b>Origin</b>	<b>Life cycle</b>	<b>Type</b>	<b>Total floral units</b>	<b>N blocks observed</b>
<i>Achillea millefolium</i>	Non-native	Perennial	Weedy	36	3
<i>Aegopodium podagraria</i>	Non-native	Perennial	Ornamental	45	2
<i>Agastache foeniculum</i>	Native	Perennial	Ornamental	250	3
<i>Ageratina altissima</i>	Native	Perennial	Ornamental	6	2
<i>Ajuga reptans</i>	Non-native	Perennial	Ornamental	4	2
<i>Alcea rosea</i>	Non-native	Perennial	Ornamental	79	8
<i>Allium</i>		Perennial	Ornamental	745	6
<i>Anethum graveolens</i>	Non-native	Annual	Ornamental	45	2
<i>Antirrhinum majus</i>	Non-native	Annual	Ornamental	460	12
<i>Aquilegia canadensis</i>	Native	Perennial	Ornamental	99	7
<i>Arctium lappa</i>	Non-native	Perennial	Weedy	213	5
<i>Aruncus dioicus</i>	Native	Perennial	Ornamental	132	2
<i>Asclepias syriaca</i>	Native	Perennial	Ornamental	106	2
<i>Asclepias tuberosa</i>	Native	Perennial	Ornamental	292	5
<i>Astilbe chinensis</i>	Non-native	Perennial	Ornamental	129	6
<i>Begonia</i>	Non-native	Annual	Ornamental	5208	32
<i>Brassica rapa</i>	Non-native	Annual	Ornamental	30	2
<i>Buddleja davidii</i>	Non-native	Perennial	Ornamental	46	3
<i>Campanula rapunculoides</i>	Non-native	Perennial	Ornamental	1937	11
<i>Campsis radicans</i>	Native	Perennial	Ornamental	294	6
<i>Capsicum anuum</i>	Non-native	Annual	Ornamental	78	6
<i>Carduus nutans</i>	Non-native	Perennial	Weedy	18	7
<i>Catharanthus roseus</i>	Non-native	Annual	Ornamental	35	2
<i>Celosia argentea</i>	Non-native	Annual	Ornamental	158	14
<i>Centaurea cyanus</i>	Non-native	Annual	Ornamental	43	2
<i>Centaurea montana</i>	Non-native	Perennial	Ornamental	23	2
<i>Cerastium vulgatum</i>	Non-native	Perennial	Weedy	219	3

<i>Cichorium intybus</i>	Non-native	Perennial	Weedy	590	13
<i>Cirsium arvense</i>	Non-native	Perennial	Weedy	22	3
<i>Clematis</i>		Perennial	Ornamental	261	7
<i>Cleome hassleriana</i>	Non-native	Annual	Ornamental	34	3
<i>Commelina</i>					
<i>communis</i>	Non-native	Annual	Weedy	698	25
<i>Conoclinium</i>					
<i>coelestinum</i>	Native	Perennial	Ornamental	141	5
<i>Consolida ajacis</i>	Non-native	Annual	Ornamental	18	2
<i>Convolvulus</i>					
<i>arvensis</i>	Non-native	Perennial	Weedy	3780	26
<i>Coreopsis</i>	Native	Perennial	Ornamental	680	23
<i>Coronilla varia</i>	Non-native	Perennial	Weedy	11	2
<i>Corydalis lutea</i>	Non-native	Perennial	Ornamental	14	2
<i>Cosmos bipinnatus</i>	Non-native	Annual	Ornamental	162	9
<i>Cucumis sativus</i>	Non-native	Annual	Ornamental	105	3
<i>Cucurbita pepo</i>	Non-native	Annual	Ornamental	66	4
<i>Cyclamen persicum</i>	Non-native	Annual	Ornamental	73	2
<i>Dahlia</i>	Non-native	Annual	Ornamental	24	5
<i>Daucus carota</i>	Non-native	Perennial	Weedy	332	18
<i>Dianthus</i>	Non-native		Ornamental	1351	29
<i>Echinacea purpurea</i>	Native	Perennial	Ornamental	858	16
<i>Erigeron annuus</i>	Native	Annual	Weedy	101	3
<i>Erigeron strigosus</i>	Native	Annual	Weedy	949	16
<i>Erysimum</i>					
<i>cheiranthoides</i>	Non-native	Annual	Weedy	75	2
<i>Fuchsia</i>	Non-native	Annual	Ornamental	19	3
<i>Gaillardia x</i>					
<i>grandiflora</i>	Native	Perennial	Ornamental	243	17
<i>Galinsoga ciliata</i>	Non-native	Annual	Weedy	5550	17
<i>Geranium</i>					
<i>maculatum and</i>					
<i>cranebills<sup>a</sup></i>			Ornamental	740	9
<i>Gladiolus</i>	Non-native	Annual	Ornamental	136	7
<i>Glechoma</i>					
<i>hederacea</i>	Non-native	Perennial	Weedy	86	3
<i>Helianthus annuus</i>	Native	Perennial	Ornamental	49	2
<i>Hemerocallis</i>	Non-native	Perennial	Ornamental	648	27
<i>Heuchera sanguinea</i>	Native	Perennial	Ornamental	42	3
<i>Hibiscus syriacus</i>	Non-native	Perennial	Ornamental	654	19
<i>Hieraceium pilosella</i>	Non-native	Perennial	Weedy	168	2
<i>Hosta</i>	Non-native	Perennial	Ornamental	2328	45
<i>Hydrangea</i>	Non-native	Perennial	Ornamental	3017	36
<i>Hylotelephium</i>	Non-native	Perennial	Ornamental	460	11

*spectabile*

<i>Impatiens</i>	Non-native	Annual	Ornamental	11750	40
<i>Ipomoea purpurea</i>	Non-native	Annual	Ornamental	166	13
<i>Iris versicolor</i>	Native	Perennial	Ornamental	4	2
<i>Itea virginica</i>	Native	Perennial	Ornamental	673	4
<i>Lamium maculatum</i>	Non-native	Perennial	Ornamental	622	11
<i>Lantana</i>	Non-native	Annual	Ornamental	144	2
<i>Lathyrus latifolius</i>	Non-native	Perennial	Ornamental	39	4
<i>Lavandula</i>					
<i>angustifolia</i>	Non-native	Perennial	Ornamental	756	12
<i>Lepidium virginicum</i>	Native	Annual	Weedy	3811	38
<i>Leucanthemum</i>	Non-native	Perennial	Ornamental	407	20
<i>Liatris spicata</i>	Native	Perennial	Ornamental	143	7
<i>Ligustrum</i>					
<i>japonicum</i>	Non-native	Perennial	Ornamental	3088	3
<i>Lilium</i>		Perennial	Ornamental	931	41
<i>Linaria vulgaris</i>	Non-native	Perennial	Weedy	53	2
<i>Lobelia erinus</i>	Native	Perennial	Ornamental	3668	18
<i>Lobularia maritima</i>	Non-native	Annual	Ornamental	1070	6
<i>Lonicera japonica</i>	Non-native	Perennial	Weedy	341	3
<i>Lotus corniculatus</i>	Non-native	Perennial	Weedy	33	3
<i>Lychnis coronaria</i>	Non-native	Perennial	Ornamental	50	3
<i>Malva neglecta</i>	Non-native	Annual	Weedy	211	13
<i>Malva sylvestris</i>	Non-native	Perennial	Weedy	435	5
<i>Melilotus alba</i>	Non-native		Weedy	0	2
<i>Melilotus officinalis</i>	Non-native		Weedy	558	4
<i>Mentha spicata</i>	Non-native	Perennial	Ornamental	1571	13
<i>Monarda fistulosa</i>	Native	Perennial	Ornamental	274	10
<i>Narcissus</i>	Non-native	Perennial	Ornamental	51	2
<i>Nepeta cataria</i>	Non-native	Perennial	Ornamental	2597	16
<i>Ocimum bacilicum</i>	Non-native	Annual	Ornamental	3	3
<i>Oenothera pilosella</i>	Native	Perennial	Ornamental	145	3
<i>Oxalis stricta</i>	Native	Perennial	Weedy	2320	35
<i>Oxalis triangularis</i>	Non-native	Perennial	Ornamental	94	3
<i>Papaver</i>	Non-native	Perennial	Ornamental	37	2
<i>Pelargonium</i>	Non-native	Perennial	Ornamental	1961	39
<i>Penstemon digitalis</i>	Native	Perennial	Ornamental	65	5
<i>Peonia</i>	Non-native	Perennial	Ornamental	33	8
<i>Perovskia</i>					
<i>atriplicifolia</i>	Non-native	Perennial	Ornamental	846	6
<i>Petunia</i>	Non-native	Annual	Ornamental	11420	46
<i>Phlox divaricata</i>	Native	Perennial	Ornamental	1201	31
<i>Physalis subglabrata</i>	Native	Perennial	Weedy	55	3

<i>Phytolacca</i>					
<i>americana</i>	Native	Perennial	Weedy	56	2
<i>Plantago lanceolata</i>	Non-native	Perennial	Weedy	8702	25
<i>Plantago major</i>	Non-native	Perennial	Weedy	15912	47
<i>Platycodon</i>					
<i>grandiflorus</i>	Non-native	Perennial	Ornamental	79	7
<i>Polygonum</i>					
<i>persicaria</i>	Non-native	Annual	Weedy	2211	34
<i>Portulaca</i>					
<i>grandiflora</i>	Non-native	Annual	Ornamental	77	2
<i>Potentilla fruticosa</i>	Native	Perennial	Ornamental	1181	4
<i>Ranunculus repens</i>	Non-native	Perennial	Weedy	177	2
<i>Ratibida</i>					
<i>columnifera</i>	Native	Perennial	Ornamental	2279	3
<i>Rhododendron</i>		Perennial	Ornamental	807	6
<i>Rosa</i>		Perennial	Ornamental	11083	51
<i>Rudbeckia hirta</i>	Native	Perennial	Ornamental	1971	22
<i>Salvia elegans</i>	Non-native	Annual	Ornamental	48	19
<i>Salvia nemorosa</i>	Non-native	Perennial	Ornamental	1751	2
<i>Salvia splendens</i>	Non-native	Annual	Ornamental	1401	16
<i>Sambucus nigra</i>	Native	Perennial	Ornamental	68	2
<i>Saponaria officinalis</i>	Non-native	Perennial	Weedy	45	3
<i>Sedum acre</i>	Non-native	Perennial	Ornamental	707	12
<i>Solanum dulcamara</i>	Non-native	Perennial	Weedy	1488	30
<i>Solanum</i>					
<i>lycopersicum</i>	Non-native	Annual	Ornamental	297	10
<i>Solanum ptycanthum</i>	Native	Perennial	Weedy	156	16
<i>Solanum tuberosum</i>	Non-native	Annual	Ornamental	23	3
<i>Solenostemon</i>					
<i>scutellarioides</i>	Non-native	Annual	Ornamental	112	5
<i>Sonchus oleraceus</i>	Non-native	Annual	Weedy	610	33
<i>Spirea japonica</i>	Non-native	Perennial	Ornamental	4610	17
<i>Stachys officinalis</i>	Non-native	Perennial	Ornamental	23	2
<i>Sutera cordata</i>	Non-native	Annual	Ornamental	258	4
<i>Syringa vulgaris</i>	Non-native	Perennial	Ornamental	685	12
<i>Tagetes</i>	Non-native	Annual	Ornamental	3080	39
<i>Tanacetum</i>					
<i>parthenium</i>	Non-native	Perennial	Weedy	448	7
<i>Taraxacum</i>					
<i>officinale</i>	Non-native	Perennial	Weedy	1016	53
<i>thymus vulgaris</i>	Non-native	Perennial	Weedy	617	12
<i>Tradescantia</i>					
<i>ohiensis or</i>					
<i>occidentalis</i>	Native	Perennial	Ornamental	572	6

<i>Trifolium pratense</i>	Non-native	Perennial	Weedy	1605	13
<i>Trifolium repens</i>	Non-native	Perennial	Weedy	51008	54
<i>Verbena x hybrida</i>	Non-native	Annual	Ornamental	49	5
<i>Veronica persica</i>	Non-native	Annual	Ornamental	151	4
<i>Vinca minor</i>	Non-native	Perennial	Ornamental	36	3
<i>Viola</i> <sup>b</sup>			Ornamental	1249	18
<i>Yucca smalliana</i>	Non-native	Perennial	Ornamental	5	3
<i>Zantedeschia</i>					
<i>aethiopica</i>	Non-native	Annual	Ornamental	4	2
<i>Zinnia</i>	Non-native	Annual	Ornamental	351	10

<sup>a</sup> This genus includes wild Geraniums (i.e. *Geranium maculatum*), but we were unable to identify

all of them to the species level.

<sup>b</sup> Most plants in this genus were hybrid pansies, but several native viola were also recorded.

### **Chapter III. Weedy plants and select cultivated species create unequal pollinator visitation in an urban pollination network**

#### **Abstract**

Urban pollinators must cope with turnover in floral resources and a high level of non-native plants introduced by urban residents. Generalist foraging is believed to be a mechanism by which pollinators adapt to the disturbance in resource availability. However, few efforts have quantified how visits are distributed across plant species and attributes. Over a three year period, we investigated plant-pollinator interactions across 63 urbanized neighborhoods. We generated a measure of plant attractiveness based on the frequency of visits to plant species and evaluated the extent that plants provide overlapping function. Additionally, we investigated how expected generalist foraging influenced network level characteristics. Our results illustrated several trends in pollinator foraging and plant-pollinator network structure. The highest number of visits were recorded on ornamental and non-native plant species. However, on a per-species basis, native plants attracted a higher number of visitors. Most pollinators foraged on resources across diverse plant attributes and floral morphologies, although some apparent specialization remains among pollinating taxa. A subset of highly attractive plants resulted in a small central core of interactions that included non-native species. An unequal distribution of visits between plant species led to low nestedness and indicated how the highly modified foraging diets of urban pollinators could be conserved in as few as four plant species. Efforts to provision resources for pollinators should focus on plant species with characteristics that make them attractive to a broad range of species.

## Introduction

Pollination by animals is an important ecosystem service for food production (Klein et al. 2007) and plant reproduction for the majority of species worldwide (Ollerton et al. 2011). However, anthropogenic stressors including introduced pathogens (Cameron et al. 2011, Ravoet et al. 2014), pesticides (Sanchez-Beyo and Goka 2014), and habitat loss (Winfree et al. 2009) reduce pollinator diversity. These effects can also change functional characteristics of the pollinator assemblage (Williams et al. 2010), which creates additional risk for plants dependent on particular pollinator species (Biesmeijer et al. 2006). The effects of landscape-level change on pollinator visitation patterns are frequently studied in agro-ecosystems, where pollination services have a high economic value. However, human-driven disturbance is a major factor in other systems including cities. The unique set of ecological and socioeconomic conditions that shape urban landscapes necessitate studies of plant-pollinator interactions specific to this habitat.

Although cities are a highly disturbed ecosystem, they contain a remarkable level of plant resources for pollinators (McKinney et al. 2008, La Sorte et al. 2014). These include crops in urban agriculture (Matteson and Langellotto 2009) and cultivated plants in residential gardens (Hostetler and McIntyre 2001, Frankie et al. 2005). Urban residents contribute to plant diversity by growing plants for food and aesthetics, and the gardening practices of individual homeowners and renters can determine plant community composition (Loram et al. 2011, Knapp et al. 2012) and plant functional traits (Lowenstein and Minor 2016). Socioeconomic patterns (Hope et al. 2003, Cook et al. 2012, Grove et al. 2014) and invasion dynamics of accidental and intentional introductions (Dehnen-Schmutz et al. 2007, Kowarik and Samuel 2008) also influence plant communities. These factors favor certain types of plants that grow in blighted areas (Kowarik 2008, Lowenstein et al. in press). Many common garden plants are non-native (Knapp et al.

2012), but there also may be efforts to increase native diversity through wildlife-friendly gardening within urban areas (Goddard et al. 2013). In addition to plant origin, gardeners may prefer plants with certain traits, such as flower color, which can also mediate interactions between plants and pollinators (Giurfa et al. 1999, Herrera and Pellmyr 2002). The altered plant community in cities poses an interesting question of how pollinators use these novel resources and how cultivation practices influence plant-pollinator networks.

Over several hundred years, non-native plants have integrated into pollinator networks in various habitats (Aizen et al. 2008, Williams et al. 2011), making them a well-studied area of plant-pollinator interactions. Several common non-native garden plants remain attractive to pollinators (Garbuzov and Ratnieks 2014a). This might suggest a potential reduction in interactions with native plants (but see Frankie et al. 2005), as pollinator species readily adapt by increasing their dietary breadth and visiting non-native plants (Williams et al. 2011, Chrobok et al. 2013). In fact, generalism is a common feature of plant-pollinator networks in both intact and disturbed systems (Memmott and Waser 2002, Bascompte et al. 2003, Petanidou et al. 2008). However, there is a scarcity of data regarding how individual plant species and various plant attributes affect visitation patterns and network structure in cities. The presence of common nectar and pollen-rich cultivated species in cities (Frankie et al. 2005, Garbuzov and Ratnieks 2014a) should offer pollinators opportunities to forage across plant families and functional traits. Yet, pollinators in some urban settings have been found to visit fewer plant species relative to less urbanized areas (Jedrzejewska-Szmek and Zych 2013, Deguines et al. 2016). This modified behavior could indicate that urban pollinators may not be as generalized in foraging as expected.

We investigated foraging activity in a diverse urban plant community and its effects on network characteristics. In particular, we used three years of observations to investigate two



aspects of pollinator visitation in Chicago, IL (USA) neighborhoods. First, we compared the attractiveness of individual plant species and groups of plant species with various attributes. We investigated whether pollinators preferred plants with certain attributes or life-history traits and anticipated that the dominance of non-native plants would lead most pollinators to visit these species. Second, we looked more broadly at network-level patterns. Most networks contain interactions of varying strength with stability maintained by a core group of plant species (Bascompte and Jordano 2007). We examined nestedness and connectance in the urban network and whether non-native plants dominated this core of connections. Finally, we investigated how specialized individual pollinators were in their visitation patterns and how this influenced network characteristics. By examining multiple years of plant-pollinator interactions, we sought to identify how pollinators distribute visits across an urbanized landscape.

## **Methods**

### *Sample sites*

We evaluated plant-pollinator interactions in 63 urban neighborhoods over three years in and around Chicago, IL. In 2011, 28 sites were visited three times between July 7 and August 22. In 2012, the same sites as well as an additional 5 sites were visited two times between June 18 and August 27. In 2013, we visited all of the previous 33 sites and an additional 30 sites twice between June 10 and August 21. In a given summer, site visits were separated by at least 20 days. Sites were selected to include a range of neighborhoods with different development intensities and socioeconomic characteristics. With the exception of one pair of sites, all sites were at least 585 m apart (average distance = 1798 m).

### *Plant and pollinator data collection*

We used a transect-based sampling approach to count all flowers along a 150 x 5 m path

paralleling the sidewalk. Inflorescences, racemes, umbels, and floral clusters were treated as a single floral unit (Baldock et al. 2015). All flowers were identified in the field to the species or genus level, or photos were taken for later identification. As we observed flowers, we recorded pollinators (aculeate bees and Diptera: Syrphidae) that contacted the plants' reproductive structures for at least 1 second. Although this does not always equate to a pollination event, pollinator visits are a useful proxy for pollination services (Vázquez et al. 2005). In the first year of sampling, pollinators were collected and identified to species (Lowenstein et al. 2014), but we avoided collecting specimens on private property. In subsequent years, pollinators were identified to the lowest possible taxonomic level in the field. To maintain a consistent taxonomic resolution across years, all pollinator-level analyses were performed at the genus level with the exception of the following easily recognizable bees identified to species level: bumble bees, *Apis mellifera*, *Agapostemon virescens*, *Anthidium manicatum*, *Augochlora pura*, *Halictus ligatus*, *Melissodes bimaculata*, and *Xylocopa virginica*. Hereafter, we use the term “morpho-types” to describe pollinator taxa. We sampled plants and pollinators on days with full to partial sun between the hours of 9:00-16:00.

By using transect-based sampling, unequal sample time is allocated per plant species. Abundant plant species would be observed more frequently than less-common plant species. However, studies suggest that transect and timed-observation methods do not affect the higher-level network properties of connectance and nestedness (Gibson et al. 2011).

We classified plants by three plant functional traits: life cycle (perennial or annual), origin to the USA east of the Rocky Mountains (native or non-native), and cultivation intent (weedy—most likely spontaneous, or ornamental—most likely deliberately planted). We used field guides and the Missouri Botanic Garden plant finder

(<http://www.missouribotanicalgarden.org/plantfinder/plantfindersearch.aspx>) to classify plants by life cycle and origin. Additionally, we classified plants according to the floral characteristics of symmetry and color. We classified flower petal color as white/pink, red, yellow/orange, or blue/purple. Species with multiple colors on petals were excluded from this portion of the analysis, as were plants with different-colored cultivars (the omitted species made up 24% of all species investigated). We classified floral symmetry as radial or bilateral using field guides and Discover Life (<http://www.discoverlife.org/20/q?search=Plantae>).

### *Data analysis*

We used all observations collected from the 63 neighborhoods to conduct several analyses on the effect of plant traits and floral characteristics on pollinator visitation. We compared the number of pollinator visits and richness of visitors by plant traits and floral symmetry with Mann-Whitney Wilcoxon tests. Abundance and richness on each plant species were averaged over the number of sampling events when a plant was observed, to reduce bias from uneven sampling. To compare number of visits and richness by flower color, we used one-way ANOVAs with response variables log-transformed to improve normality. Because only four plant species had red flowers, we excluded red flowers from color-preference analyses.

To investigate if pollinator visitation varied based on plant traits (cultivation intent, life cycle, origin) or floral characteristics (color, symmetry), we compared the proportion of plant species with each trait that were visited at least once by a pollinator (presence or absence). We performed separate analyses for each trait or characteristic using two-tailed tests of population proportion. Additionally, we identified plant species with higher pollinator richness than would be expected based on their floral abundance. To identify these highly-visited plant species (hereafter called ‘attractive’ species), we used least squares regression, with variables log-

transformed, classifying attractive species as those appearing above the 95% confidence intervals (Harmon-Threatt and Hendrix 2015).

#### *Network construction and analysis*

We used all plant-pollinator observations to create a bipartite plant-pollinator network with links weighted by the number of observed interactions between each plant and pollinator (bipartite package in R 3.1; Dormann et al. 2009). We also examined binary networks, with unweighted links, but results did not vary substantially and are not reported here. Each link represented a potential pollination event. To determine the influence of cultivation practices on plant-pollinator interactions, we investigated network structure for the complete network as well as sub-networks for each plant and floral attribute.

To determine resource-use patterns in the urban plant-pollinator network, we calculated two parameters that characterize interactions. Pollinator specialization index ( $d'$ ) measures how strongly a pollinator's interactions deviate from a random selection of plants (Bluthgen et al. 2006). The output ranges from 0 (no specialization) to 1 (complete specialization on a plant host). Connectance is the number of observed links in the network divided by the number of cells in the network matrix (Jordano 1987).  $d'$  was calculated based on visits to the complete network, while connectance was calculated for the sub-network of each plant and floral attribute.

We also analyzed the matrix structure of the network using nestedness (NODF; Almeida-Neto et al. 2008). Nestedness measures network organization, expressing the tendency of specialist species to interact with a subset of the interaction partners of more generalist species (Bascompte et al. 2003). Values range between 0 (random structure) and 100 (complete nestedness). For this analysis, plant-pollinator interactions were converted to binary values. To investigate if network structure was more nested than a random network with the same

dimensions, we generated 999 replicates of a null model based on the probability of an interaction being proportional to the degree of generalization in plants and pollinators (null model 2 in Bascompte et al. 2003). Null model analysis was performed in ANINHADO (Guimaraes and Guimaraes 2006). We used a one sample t-test to compare nestedness of the observed networks to the randomly generated networks.

### *Extinction simulation*

To investigate how the loss of plant species would impact pollinators, we simulated plant extinction for the complete plant-pollinator network using the `second.extinct` function in the `bipartite` package. We used a model that removed plant species systematically from the least to most abundant. As plants are removed, the simulation recorded when a pollinator extinction event occurred. From this information and evaluating the links between plants and pollinators, we constructed a reduced network that would include the minimal number of plant species that potentially supports all pollinating insects.

## **Results**

Over three years, we recorded 1,815 pollinator visits from 24 pollinator morpho-types to 106 plant taxa (Appendix 1). An additional 57 plant taxa were recorded on transects but were not visited by pollinators. There was no significant difference in the proportion of plant species from each trait with and without a pollinator visit. Flower color was the exception; pollinators visited a greater proportion of yellow than white flowers ( $\chi^2=7.93$ ,  $P=0.005$ ; Fig. 1). Plant species with the most pollinator visits included *Trifolium repens* (6.7% of visits), *Convolvulus arvensis* (6.2% of visits), and *Hibiscus syriacus* (5.0% of visits). The highest pollinator morpho-type richness was observed on *C. arvensis* ( $N = 17$ ) and *Rudbeckia hirta* ( $N = 16$ ). Pollinator morpho-types with the most floral visits included *Toxomerus* spp. (17%), *Lasioglossum* spp. (15.1%), and *Apis*

*mellifera* (13.4%). The highest number of plant species were visited by *Lasioglossum* spp. and *Bombus impatiens* (N = 63 and N = 48, respectively).

Most plants in the network were non-native, perennial, and ornamental, and most pollinator visits were recorded on plants with these traits (Table 1). Flowers tended to be purple or white and have radial symmetry. Pollinator abundance was significantly greater in native than non-native flowers (W=1152, P=0.05, Fig. 2). Pollinator abundance was also greater on perennial than annual flowers (W=757, P=0.02). There was no difference in pollinator abundance between plants of ornamental or weedy plants (W=1186, P=0.87), plants with bilateral or radial floral symmetry (W=946, P=0.60), or plants with different flower colors (F=0.48, P=0.62). Pollinator morpho-type richness was significantly greater in ornamental than weedy flowers (W=1589, P=0.003). There were no significant differences in pollinator richness by origin (W=1127, P=0.08), life cycle (W=922, P=0.23), symmetry (W=1040, P=0.85), or color (F=1.03, P=0.36). Forty-two plant species were more attractive to pollinators than would be expected based on their floral abundance (Fig. 3, Appendix 1). The top pollinator-attractive plants, identified from model residuals, included the following species: *C. arvensis*, *H. syriaca*, *Nepeta cataria*, *R. hirta*, and *Salvia nemorosa*.

#### *Network analysis*

On average, each pollinator taxon or morpho-type visited 19 plant species. Yet, most plant species were visited by few pollinator morpho-types (mean  $\pm$  SE =  $4.5 \pm 0.36$ , Appendix 2). As a result, only around 20% of connections were realized in the complete network and in the sub-networks for each plant functional trait (Table 1). The only notable outlier in this respect were plants with purple flowers, which comprised the most connected sub-network (connectance = 0.27). None of the networks were more nested than their random permutations (t = 0.01-0.02, P

= 0.97-0.99).

For pollinators with at least 5 observations, floral specialization ( $d'$ ) ranged from generalized (0) to somewhat specialized (0.70; Appendix 3). *Melissodes bimaculata* and *Syrphus* spp. were the most generalized pollinators and *Xylocopa virginica* and *Andrena* spp. were the most specialized.

#### *Extinction simulation*

Pollinator extinction occurred at a slow rate in systematic removal of plants from least to most common. Few morpho-types became extinct until the removal of the most frequently visited plant species, since all pollinators, except for *Coelioxys* spp., had links to multiple plant species. Several potential combinations of plant species could support all pollinator taxa in a reduced network. As few as four plant species would maintain all connections in the plant-pollinator network (Fig. 4).

#### **Discussion**

Cities offer many diverse floral resources to pollinators. Yet in Chicago neighborhoods, pollinator visitation was distributed unevenly among species and plant groups. Perennial and native plant species received more pollinator visits than their counterparts, while ornamental species were visited by more pollinator species than weedy species. A reduced plant community of only four species, two of which are considered ‘weeds’ by most gardeners, linked to the entire suite of pollinators. Finally, plant-pollinator networks in these neighborhoods were no more nested than randomly-generated networks. Together, our results reveal some unexpected aspects of the urban plant-pollinator assemblage.

#### *Visitation to plants with different traits*

Pollinator visitation and richness were considerably reduced in annual plant species.

Nearly two thirds of visited annual plant species were ornamentals and a higher percentage of unvisited annuals were also intentionally cultivated. The most common annual species, Petunia, Begonia, and Pelargonium, were present at > 50% of sites, but none were classified as attractive to pollinators based on the least squares regression analysis. Limited visitation to annual, ornamental is explained by breeding patterns that favor showiness at the expense of access to nectar or pollen (Comba et al. 1999). These species are popular in residential gardens, because they can be grown in pots, retain their color, and bloom for much of the summer months. However, if pollinator conservation is a goal, our results indicate that these most frequently cultivated annual species not the best choices for urban landscaping.

The dominance of non-native plants resulted in nearly 70% of recorded pollinator visits to this group of plants with this origin. Yet, the lack of independence between plant traits meant that the distribution of pollinator visits was influenced by several highly abundant weedy species. Weeds' ability to reproduce rapidly, withstand soil contamination (Rother et al. 1983, Simon et al. 1996) and tolerate shaded conditions (Sutherland 2004) allows several of the most common species to thrive across neighborhoods. In fact, certain widespread species, such as white clover, comprise a majority of collected pollen source in two species of urban solitary bees (MacIvor et al. 2014). Although non-native weeds did not attract the highest pollinator visitation on a per-species basis, and their ability to attract pollinators at a comparable rate to native plants depends on successful naturalization (Razanajatovo et al. 2015).

#### *Specialization and 'attractiveness' in the urban plant-pollinator network*

Several shared attributes made multiple plant species attractive to a rich group of pollinators. First, many plants identified as attractive often had inflorescences or dense floral structures and were recorded in clustered patches. Yet the number of visits per plant can be



greater in less dense floral patches (Mustajarvi et al. 2001), and further research is needed to identify if high visitation in attractive plants was due to the same individuals on foraging bouts or due to recruitment of new individuals. Second, many attractive species were perennials, flowering across multiple years, which increases the potential for long-term preferences in resource acquisition. Finally, yellow flowers were associated with a greater potential for a pollinator visit, but this could be confounded by this color's frequency in Asteraceae, a family with capitula that attract a rich pollinator community (Tuell et al. 2008, Deguines et al. 2016). Our measure of plant attractiveness included plants commonly recommended to benefit pollinating insects (Tuell, et al. 2008 Garbuzov and Ratnieks 2014b). The presence of these plants in neighborhoods indicates positive efforts to enhance pollinator resources.

Pollinator preferences towards certain plant characteristics may explain why several urban pollinators retained a degree of apparent specialization. Specialized foraging preferences remain could be due to seasonal complementarity – flowering at discrete months or times of day- (Bluthgen and Klein 2011), floral morphology barriers (Stang et al. 2009), and differences in nutritional quality. We found instances of each example through field observations and floral specialization indices. *Andrena* spp. is one of the few pollinator taxa active during spring, and its specialization is associated with visits to ephemerals and cultivated plants blooming in the early-season. The large-bodied carpenter bee, *Xylocopa virginica*, restricted visits to tubular flowers with deep nectaries including *Lilium*. *Hylaeus* is thought to be a generalist forager, but its interactions were skewed towards one plant species that appeared in the reduced network - *Daucus carota*. The small compound umbels on this flowering plant are favored by small-bodied bees to the extent that foraging records in Toronto, Canada show complete specialization by the non-native, *H. punctatus*, on this plant species (Sheffield et al. 2011). Even generalist pollinators

exhibit a tendency to partition resources based on phylogenetic or morphological preferences (Frund et al. 2010), and these apparent specializations can extend to non-native plants.

#### *Network structure in complete and sub-networks*

Several features of the urban plant-pollinator network differed from those reported in the literature. In most networks, pollinator diversity outnumbers plant diversity by as much as a 6:1 ratio (Vázquez et al. 2009), but we noted the opposite pattern even when pollinators were identified to the species level in Lowenstein et al. (2014). In this study, the percentage of connected links was comparable to studies with high sampling effort and plant species richness (Jordano 1987, Nielsen and Bascompte 2007). Many plant-pollinator networks have a central core of interactions that include non-native species (Bascompte et al. 2003), and the core of interacting species was especially limited in this study. A combination of infrequent visitation to most plants and the tendency of most pollinators to visit super-abundant and super-generalized plant species (defined by Vázquez and Aizen 2004, Williams et al. 2011) restricted most visits to a small group of plants. The presence of non-native species in this group confirms Aizen et al.'s (2008) finding that the generalist core of interactions can be transferred to non-native plants in invaded networks.

While a core of generalist plants often appears in nested networks, nestedness is dependent on an interacting subset of specialists. However, few specialists were recorded in this study and in other urban areas (Jedrzejewska-Szmek and Zych 2013, Deguines et al. 2016) included few specialists. Consequently, the absence of true specialists caused network structure to resemble a minimally nested network (see figure 1d in Almeida-Neto and Ulrich 2011). In addition to generalized foraging, our use of NODF as a measurement (Joppa et al. 2010) may explain why nestedness differed from other published networks (Ollerton et al. 2003, Fontaine et

al. 2006, Chacoff et al. 2012). While non-nested networks are less cohesive (Bascompte and Jordano 2007), cultivation of ornamentals in urbanized landscapes appears to buffer pollinator decline through the presence of multiple complementary resources.

The extinction simulation and low pollinator morpho-type richness in most plants demonstrated a high level of redundancy in floral resources. While pollinators visited over 100 plant species, as few as four species from the complete network may support the entire pollinator community. One minimal plant assemblage included *R. hirta*, *C. arvensis*, *D. carota* and *A. cannabinum*. The first three were selected due to their floral morphology and widespread distribution that attracted a high number of pollinator taxa. *A. cannabinum*, was selected due to being the sole link with a cleptoparasitic pollinator taxa. The results of the extinction simulation should not be interpreted as a call to focus plant conservation on this narrow pool of species. Rather, it demonstrates how unequal resource quality limited pollinators to a core group of plants and potentially causes overlap in plant function.

### *Conclusion*

Anthropogenic disturbance and cultivation by humans has added many novel floral resources to the urban system, but not all are highly utilized by pollinators. Many plants were visited infrequently due to pollinator preferences related to plant distribution and attributes. These preferences led to an unequal distribution of visits to plants of different origin and cultivation intent, which in turn altered network-level features. Several plant attributes were highly supportive of pollinator visits. Native and perennial plants had the highest number of plant visitors, and this is related to characteristics of the most common plant species with these attributes. In the absence of more attractive resources, adventive weeds can contribute to stable mutualist networks (Rollin et al. 2016). However, their composition in the floral community

could also create competition for pollination among plants (Hennig and Ghazoul 2011), warranting caution. Since a high number of visited plant species were included in the network, it is unlikely that foraging pollinators are resource-limited. To provision resources for urban pollinators, we advocate for the recommendations of Salisbury et al. (2015) to include native or non-native plants with horticultural value, but not from annual life cycles.

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## TABLES

Table 1. Statistics for complete plant-pollinator network and sub-networks created from each plant and flower trait.

Network	N visits	Number plant species	Number pollinator species	Connectance	NODF*
Complete	1823	106	25	0.183	26.88
Cultivation intent					
Weedy	773	31	23	0.213	30.07
Ornamental	1050	75	24	0.186	25.91
Life cycle					
Annual	268	31	16	0.202	19.86
Perennial	1484	70	25	0.210	51.40
Origin					
Non-native	1310	76	23	0.196	26.61
Native	380	24	22	0.216	27.53
Flower color					
Purple	662	22	28	0.268	27.99
White	485	21	21	0.215	27.82
Yellow	343	21	21	0.215	21.14
Floral symmetry					
Bilateral	456	22	29	0.210	22.51
Radial	915	25	70	0.178	18.84

\* nestedness values did not differ from randomly generated networks

## FIGURES

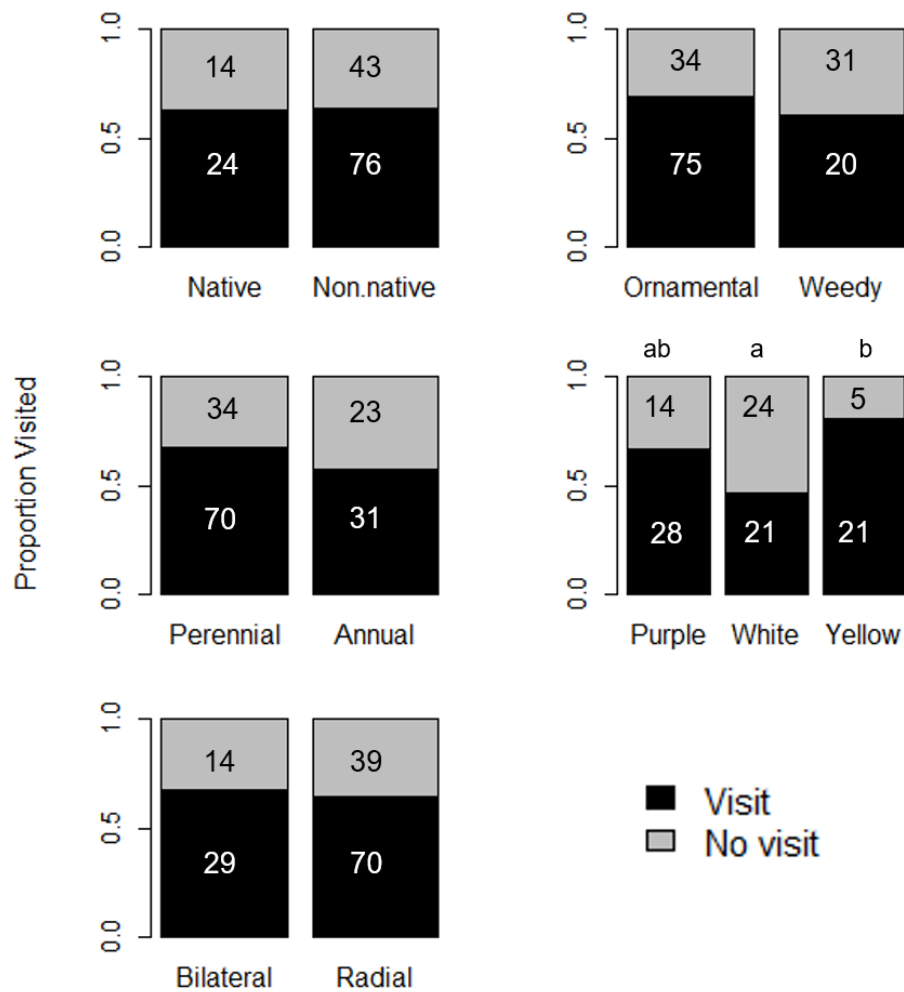


Figure 1. Proportion of plant species with and without recorded pollinator visits. Each set of bars is grouped by plant trait or floral characteristic with number of visited and not visited species listed within each bar. Plant species that could not be classified by trait were excluded from this analysis. Letters above bars indicate significant differences in proportion of plant species visited by pollinators.

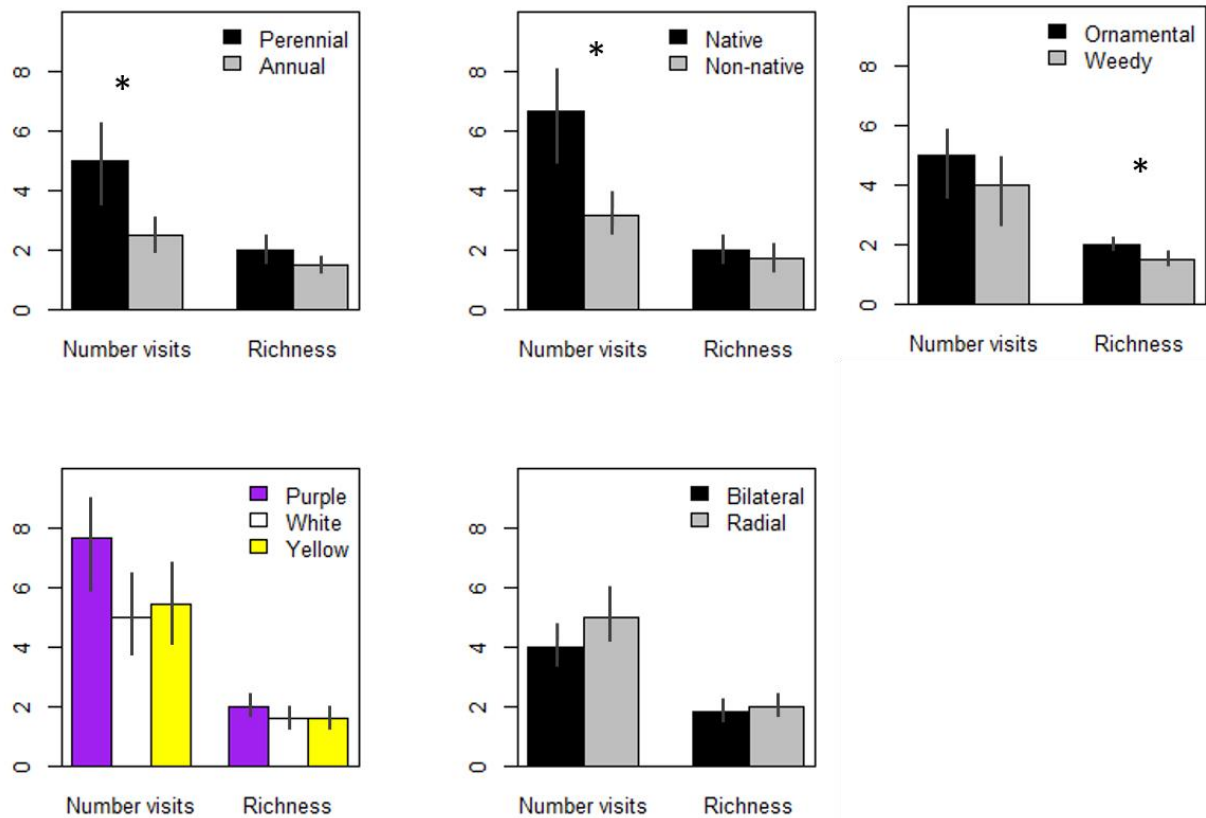


Figure 2. Median ( $\pm 95\%$  CI) weighted number of pollinator visits and morpho-type richness by plant functional trait, in first row, and flower characteristics, in second row. Asterisks indicate a significant difference ( $P \leq 0.05$ ).

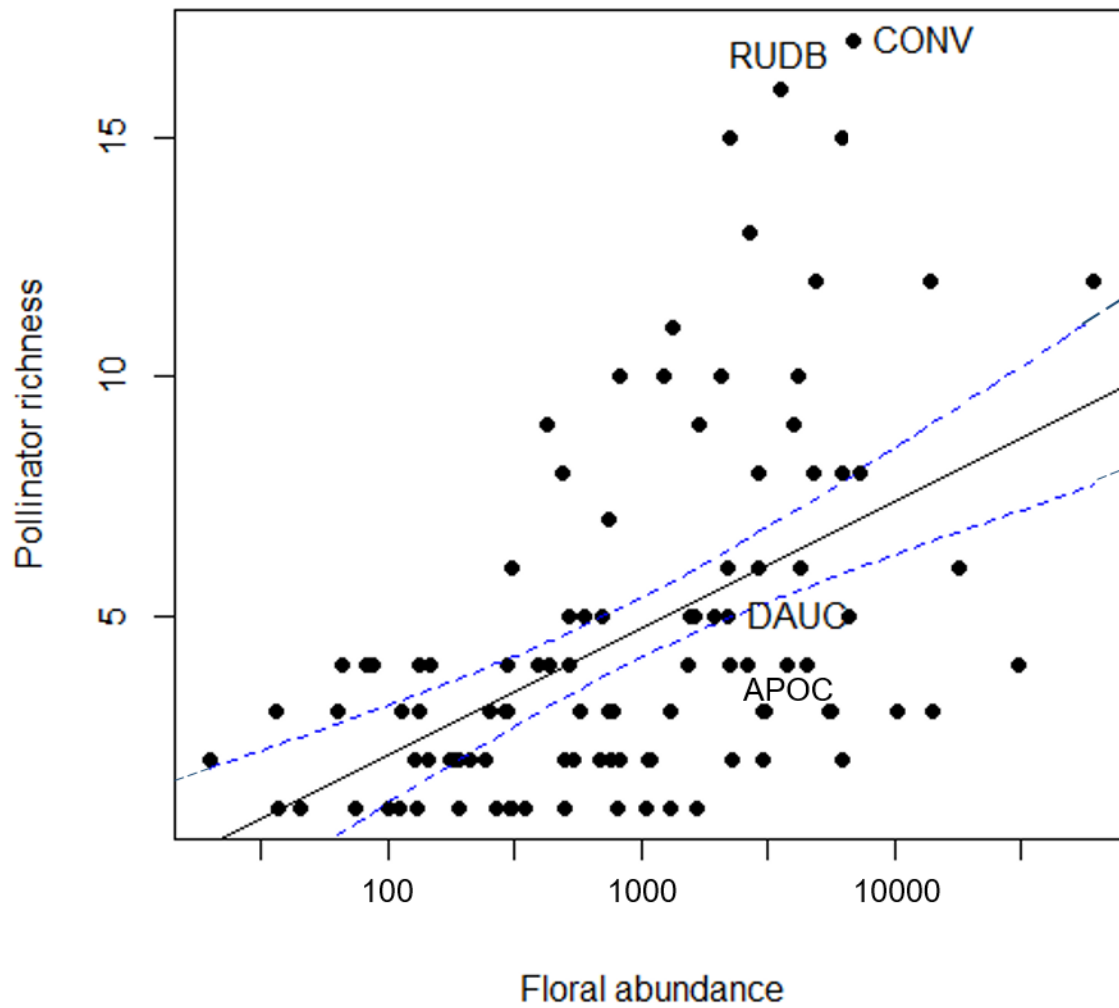


Figure 3. Regression of floral abundance of each visited plant species versus pollinator richness. Slope and 95% confidence limits plotted in logarithmic scale with axes labeled in untransformed scale. Species above the 95% CI and included in reduced network simulation are labeled. Full list of species above 95% CI are noted in Appendix 1. APOC = *Apocynum cannabinum*, CONV = *Convolvulus arvensis*, DAUC = *Daucus carota*, and RUDB = *Rudbeckia hirta*.

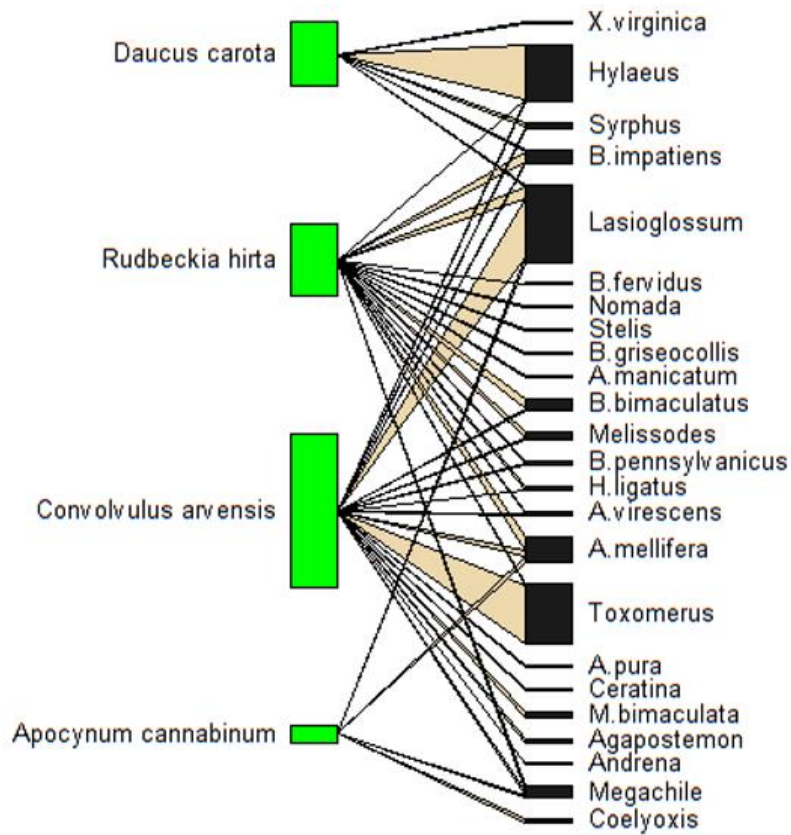


Figure 4. Plant-pollinator network based on extinction simulation, showing one combination of minimum number of plants (left) from a reduced network whose connections would supports all pollinator species (right). Full pollinator species names listed in Appendix 3. Bar size corresponds to weighted abundance of plants and pollinators with bar width corresponding to number of pollinator visits.

## APPENDICES

Appendix 1. Plants recorded on neighborhood blocks. Degree is the number of plant species visited by a pollinator taxa. Empty cells indicate that we were unable to objectively classify a plant by functional trait. Asterisk (\*) indicates that plant is classified as attractive by appearing above 95% CI from regression analysis in Figure 3.

Plant	Degree (i.e., pollinator richness)	Total recorded visits	Neighborhoods with pollinator observation	Neighborhoods with plant record	Origin	Life cycle	Type	Color	Symmetry
<i>Abelmoschus esculentus</i>	0	0	0	1	Exotic	Annual	Ornamental		Radial
<i>Abutilon pictum</i>	0	0	0	2	Exotic	Annual	Ornamental	Yellow	Radial
<i>Achillea millefolium</i>	3	10	4	14	Exotic	Perennial	Weedy	White	Radial
<i>Aegopodium podagrarea</i>	1	1	1	2	Exotic	Perennial	Ornamental	White	Radial
<i>Agastache foeniculum</i>	10	35	5	6	Native	Perennial	Ornamental	Purple	Bilateral
<i>Ageratum spp.</i>	0	0	0	12	Exotic	Annual	Ornamental	Purple	Radial
<i>Ajuga reptans</i>	0	0	0	2	Exotic	Perennial	Ornamental	Purple	Bilateral



<i>Alcea rosea</i>	2	2	1	10	Exotic	Perennial	Ornamental		Radial
<i>Allium spp.*</i>	10	72	4	7		Perennial	Ornamental	Purple	Radial
<i>Antirrhinum spp.</i>	1	1	1	14	Exotic	Annual	Ornamental		Bilateral
<i>Apocynum cannabinum</i>	4	12	1	1	Native	Perennial	Ornamental	White	Radial
<i>Aquilegia canadensis</i>	1	1	1	7	Native	Perennial	Ornamental	Red	Radial
<i>Arctium lappa*</i>	8	31	5	8	Exotic	Perennial	Weedy	Purple	Radial
<i>Asclepias syriaca</i>	4	15	3	4	Native	Perennial	Ornamental	Purple	Radial
<i>Asclepias tuberosa*</i>	5	17	3	6	Native	Perennial	Ornamental	Yellow	Radial
<i>Astilbe</i>	2	5	2	6	Exotic	Perennial	Ornamental	Red	Radial
<i>Begonia</i>	2	3	5	33	Exotic	Annual	Ornamental		Radial
<i>Buddleja davidii</i>	2	5	1	6	Exotic	Perennial	Ornamental		Radial
<i>Calystegia sepium</i>	0	0	0	6	Native	Perennial	Weedy	White	Radial
<i>Campanula rapunculoides</i>	4	11	5	14	Exotic	Perennial	Ornamental	Purple	Radial
<i>Campsis radicans*</i>	4	14	2	6	Native	Perennial	Ornamental	Red	Radial
<i>Capsicum</i>	0	0	0	8	Exotic	Annual	Ornamental	White	Radial
<i>Carduus nutans</i>	0	0	0	13	Exotic	Perennial	Weedy	Purple	Radial

<i>Catharanthus roseus</i>	0	0	0	2	Exotic	Annual	Ornamental		Bilateral
<i>Celosia</i>	2	5	3	14	Exotic	Annual	Ornamental		Radial
<i>Centaurea cyanus</i>	0	0	0	3	Exotic	Annual	Weedy	Purple	
<i>Centaurea montana*</i>	3	3	2	4	Exotic	Perennial	Ornamental		Radial
<i>Chamerion angustifolium</i>	0	0	0	1	Native	Perennial		Purple	Radial
<i>Chenopodium spp.</i>	0	0	0	2	Exotic	Annual	Weedy	White	Radial
<i>Cichorium intybus*</i>	8	48	6	17	Exotic	Perennial	Weedy	Purple	Radial
<i>Cirsium arvense</i>	0	0	0	3	Exotic	Perennial	Weedy	Purple	Radial
<i>Clematis</i>	0	0	0	12	Exotic	Perennial	Ornamental	Purple	Radial
<i>Cleome hassleriana*</i>	4	5	2	5	Exotic	Annual	Ornamental		Bilateral
<i>Commelina communis</i>	1	1	2	26	Exotic	Annual	Weedy	Purple	Bilateral
<i>Consolida ajacis</i>	0	0	0	3	Exotic	Annual	Weedy	Purple	Bilateral
<i>Convolvulus arvensis*</i>	17	112	17	26	Exotic	Perennial	Weedy	Purple	Radial
<i>Coreopsis*</i>	9	27	8	31	Native	Perennial	Ornamental	Yellow	Radial
<i>Corydalis lutea</i>	0	0	0	2	Exotic	Perennial	Weedy	Yellow	Bilateral
<i>Cosmos bipinnatus*</i>	7	16	4	12	Exotic	Annual	Ornamental	White	Radial

<i>Cucumis sativus*</i>	3	5	3	4	Exotic	Annual	Ornamental	Yellow	Radial
<i>Cucurbita pepo*</i>	4	6	2	6	Exotic	Annual	Ornamental	Yellow	Radial
<i>Cyclamen persicum</i>	0	0	0	3	Exotic	Annual	Ornamental	White	
<i>Dahlia*</i>	3	4	1	10	Exotic	Annual	Ornamental		Radial
<i>Dalibarda repens</i>	0	0	0	1	Native	Perennial	Weedy	White	Radial
<i>Datura stramonium</i>	0	0	0	1	Exotic	Annual	Weedy	White	Radial
<i>Daucus carota</i>	5	46	13	27	Exotic	Perennial	Weedy	White	Radial
<i>Dianthus</i>	1	1	1	33	Exotic		Ornamental		Radial
<i>Dodecatheon meadia</i>	0	0	0	1	Native	Perennial	Ornamental	White	Radial
<i>Echinacea purpurea*</i>	11	39	11	23	Native	Perennial	Ornamental	Purple	Radial
<i>Echinocystis lobata</i>	0	0	0	1	Native	Annual		White	Radial
<i>Erigeron annuus*</i>	3	5	1	7	Native	Annual	Weedy	White	Radial
<i>Erigeron strigosus</i>	3	7	4	22	Native	Annual	Weedy	White	Radial
<i>Erysimum cheiranthoides</i>	1	2	1	2	Exotic	Annual	Weedy	Yellow	Radial
<i>Fritillaria thunbergia</i>	0	0	0	1	Exotic	Perennial	Ornamental		Radial
<i>Fuchsia</i>	0	0	0	3	Exotic	Annual	Ornamental		Radial
<i>Gaillardia</i>	2	2	2	17	Native	Perennial	Ornamental		Radial

<i>Galinsoga ciliata</i>	3	4	4	17	Exotic	Annual	Weedy	White	Radial
<i>Galium odoratum</i>	0	0	0	1	Exotic	Perennial	Weedy	White	Radial
<i>Gaura lidheimeri</i>	0	0	0	3	Native	Perennial	Ornamental	White	Bilateral
<i>Geranium maculatum</i>	2	3	2	9			Ornamental	White	Radial
<i>Gerbera</i>	0	0	0	1	Exotic	Annual	Ornamental		Radial
<i>Gladiolus</i>	2	2	1	8	Exotic	Annual	Ornamental		Bilateral
<i>Helianthus annuus*</i>	9	25	4	8	Native	Perennial	Ornamental	Yellow	
<i>Hemerocallis</i>	2	2	3	37	Exotic	Perennial	Ornamental	Yellow	
<i>Hibiscus syriaca*</i>	15	91	14	22	Exotic	Perennial	Ornamental		Radial
<i>Hieracium pilosella</i>	0	0	0	3	Exotic	Perennial	Weedy	Yellow	Radial
<i>Hosta*</i>	12	31	18	53	Exotic	Perennial	Ornamental		Radial
<i>Hoya carnososa</i>	0	0	0	1	Exotic	Annual	Ornamental		Radial
<i>Hydrangea*</i>	9	14	4	38	Exotic	Perennial	Ornamental		
<i>Hylotelephium erythrostictum*</i>	6	30	5	12	Exotic	Perennial	Ornamental	White	Radial
<i>Impatiens</i>	3	7	5	45	Exotic	Annual	Ornamental		Radial
<i>Impatiens balsamina*</i>	2	2	1	1	Exotic	Annual	Ornamental		Radial

<i>Ipomoea purpurea*</i>	4	5	3	19	Exotic	Annual	Ornamental	Purple	Radial
<i>Iris</i>	0	0	0	2	Native	Perennial	Ornamental	Purple	
<i>Itea virginica</i>	0	0	0	4	Native	Perennial	Ornamental	White	Radial
<i>Jacobaea maritima</i>	0	0	0	1	Exotic	Perennial	Ornamental	Yellow	Radial
<i>Lablab purpureus</i>	0	0	0	2	Exotic	Annual	Ornamental	Purple	Bilateral
<i>Lactuca canadensis</i>	3	5	2	7	Exotic	Perennial	Weedy	Yellow	Radial
<i>Lamium amplexicaule*</i>	3	3	1	2	Exotic	Annual	Weedy	Purple	Bilateral
<i>Lamium maculatum</i>	2	3	3	11	Exotic	Perennial	Ornamental	Purple	Bilateral
<i>Lantana</i>	0	0	0	3	Exotic	Annual	Ornamental		Radial
<i>Lathyrus</i>	1	1	1	8	Exotic	Perennial	Ornamental		Bilateral
<i>Lavandula angustifolia</i>	2	3	3	12	Exotic	Perennial	Ornamental	Purple	Bilateral
<i>Lepidium virginicum</i>	3	37	17	41	Native	Annual	Weedy	White	Radial
<i>Leucanthemum*</i>	5	12	6	22	Exotic	Perennial	Ornamental	White	Radial
<i>Liatris spicata</i>	2	3	2	7	Native	Perennial	Ornamental	Purple	
<i>Ligustrum</i>	3	3	1	3	Exotic	Perennial	Ornamental	White	Bilateral
<i>Lilium</i>	2	5	2	45		Perennial	Ornamental		Radial
<i>Linaria vulgaris</i>	1	1	1	3	Exotic	Perennial	Weedy	Yellow	Bilateral

<i>Lobelia erinus</i>	6	12	6	22	Native	Perennial	Ornamental	Purple	Bilateral
<i>Lobularia</i>	2	17	3	6	Exotic	Annual	Ornamental	White	Radial
<i>Lonicera</i>	0	0	0	6	Exotic	Perennial	Ornamental	White	Bilateral
<i>Lotus</i>									
<i>corniculatus</i>	0	0	0	5	Exotic	Perennial	Weedy	Yellow	Bilateral
<i>Lychnis</i>									
<i>coronaria</i>	0	0	0	3	Exotic	Perennial	Ornamental	Purple	Radial
<i>Malva</i>									
<i>neglecta*</i>	4	4	5	19	Exotic	Annual	Weedy	Purple	Radial
<i>Malva</i>									
<i>sylvestris*</i>	4	4	3	5	Exotic	Perennial	Weedy	Purple	Radial
<i>Mandevilla</i>									
<i>dipladenia</i>	0	0	0	1	Exotic	Annual	Ornamental		Radial
<i>Melilotus alba*</i>	7	46	4	8	Exotic		Weedy	White	Bilateral
<i>Melilotus</i>									
<i>officinalis*</i>	5	17	2	6	Exotic		Weedy	Yellow	Bilateral
<i>Mentha</i>									
<i>spicata*</i>	6	38	6	17	Exotic	Perennial	Ornamental	Purple	Bilateral
<i>Monarda</i>									
<i>fistulosa*</i>	5	14	7	11	Native	Perennial	Ornamental	Purple	Bilateral
<i>Narcissus</i>	0	0	0	2	Exotic	Perennial	Ornamental		Radial
<i>Nepeta cataria*</i>	15	71	11	19	Exotic	Perennial	Ornamental	Purple	Bilateral
<i>Ocimum</i>									
<i>bacilicum</i>	0	0	0	3	Exotic	Annual	Ornamental	White	Bilateral
<i>Oenothera</i>									
<i>pilosella</i>	2	6	1	3	Native	Perennial	Ornamental	Yellow	Radial
<i>Onopordum</i>									
<i>acanthium</i>	0	0	0	1	Exotic	Perennial	Weedy	Purple	Radial

<i>Origanum vulgare*</i>	5	34	2	3	Exotic	Perennial	Ornamental	Purple	Bilateral
<i>Oxalis stricta</i>	4	25	12	38	Native	Perennial	Weedy	Yellow	Radial
<i>Oxalis triangularis</i>	0	0	0	4	Exotic	Perennial	Ornamental	White	Radial
<i>Papaver</i>	1	1	1	2	Exotic	Perennial	Ornamental		Radial
<i>Pelargonium</i>	3	3	3	44	Exotic	Perennial	Ornamental		Radial
<i>Peonia</i>	0	0	0	8	Exotic	Perennial	Ornamental		
<i>Perovskia atriplicifolia*</i>	5	35	3	8	Exotic	Perennial	Ornamental	Purple	Bilateral
<i>Petunia</i>	6	10	6	50	Exotic	Annual	Ornamental		Radial
<i>Phlox paniculata or divaricata</i>	3	5	4	37	Native	Perennial	Ornamental		Bilateral
<i>Physalis subglabrata</i>	0	0	0	3	Native	Perennial	Weedy		Radial
<i>Physostegia virginiana</i>	0	0	0	1	Native	Perennial	Ornamental	White	Bilateral
<i>Phytolacca americana</i>	1	4	1	4	Native	Perennial	Weedy	White	Radial
<i>Plantago lanceolata</i>	6	47	13	26	Exotic	Perennial	Weedy	White	Radial
<i>Plantago major</i>	4	19	12	50	Exotic	Perennial	Weedy	White	Radial
<i>Platycodon grandiflorus</i>	1	1	1	9	Exotic	Perennial	Ornamental	Purple	Bilateral
<i>Polygonum persicaria</i>	5	25	11	42	Exotic	Annual	Weedy	White	Radial

<i>Portulaca grandiflora</i>	4	10	1	3	Exotic	Annual	Ornamental		Radial
<i>Prunella vulgaris</i>	0	0	0	1	Exotic	Perennial	Weedy	Purple	Bilateral
<i>Ranunculus</i>	2	3	1	2	Exotic	Perennial	Weedy	Yellow	Radial
<i>Ratibida columnifera</i>	2	9	2	3	Native	Perennial	Ornamental	Yellow	Radial
<i>Rhododendron</i>	1	5	1	6		Perennial	Ornamental		
<i>Rosa*</i>	12	45	16	55		Perennial	Ornamental		
<i>Rudbeckia hirta*</i>	16	53	14	27	Native	Perennial	Ornamental	Yellow	Radial
<i>Salvia elegans</i>	0	0	0	2	Exotic	Annual	Ornamental	red	Bilateral
<i>Salvia nemorosa*</i>	13	40	13	21	Exotic	Perennial	Ornamental	Purple	Bilateral
<i>Salvia splendens</i>	4	9	4	19	Exotic	Annual	Ornamental	Red	Bilateral
<i>Sambucus nigra</i>	0	0	0	2	Native	Perennial	Ornamental	White	Radial
<i>Saponaria officinalis</i>	1	1	1	5	Exotic	Perennial	Weedy	White	Radial
<i>Sedum acre</i>	5	17	3	12	Exotic	Perennial	Ornamental	Yellow	Radial
<i>Silene</i>	0	0	0	1	Exotic	Perennial	Weedy	White	Radial
<i>Solanum dulcamara*</i>	8	11	9	32	Exotic	Perennial	Weedy	Purple	Radial
<i>Solanum lycopersicum</i>	1	3	1	13	Exotic	Annual	Ornamental	Yellow	Radial
<i>Solanum nigrum</i>	0	0	0	5	Exotic	Perennial	Weedy	White	Radial
<i>Solanum</i>	0	0	0	16	Native	Perennial	Weedy	White	Radial

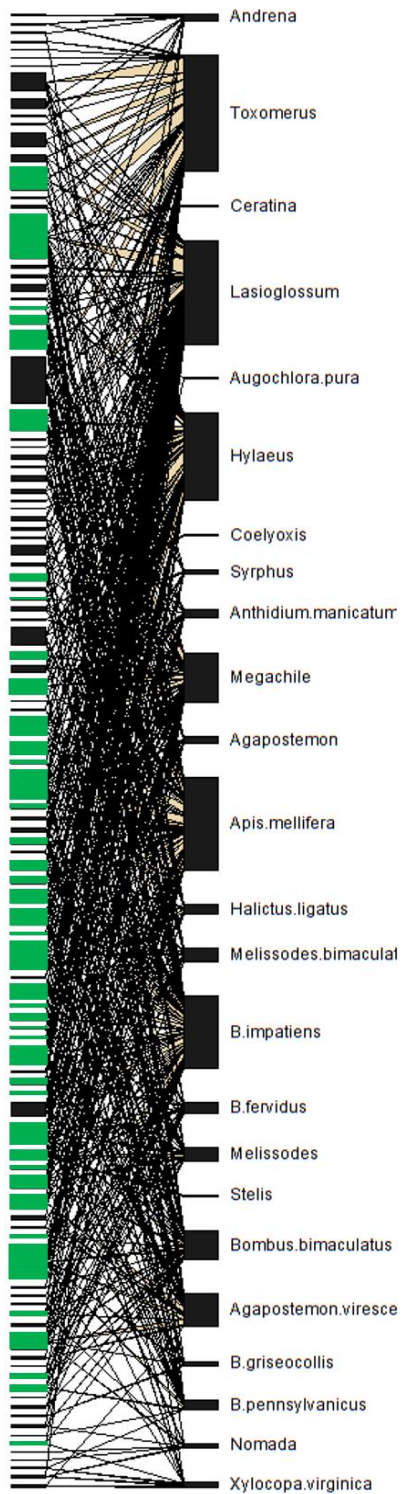


<i>ptycanthum</i>									
<i>Solenostemon scutellarioides</i>	1	1	1	5	Exotic	Annual	Ornamental	Purple	Bilateral
<i>Solidago</i>	1	1	1	2	Native	Perennial	Ornamental	Yellow	Radial
<i>Sonchus oleraceus*</i>	10	54	14	39	Exotic	Annual	Weedy	Yellow	Radial
<i>Spirea*</i>	8	16	8	18	Exotic	Perennial	Ornamental	White	Radial
<i>Stachys byzantina</i>	0	0	0	5	Exotic	Perennial	Weedy	Purple	Bilateral
<i>Sutera cordata</i>	0	0	0	4	Exotic	Annual	Ornamental	White	Radial
<i>Symphytum*</i>	4	9	1	1	Exotic	Perennial	Ornamental		Radial
<i>Syringa</i>	2	5	2	12	Exotic	Perennial	Ornamental	White	Radial
<i>Tagetes</i>	4	5	7	43	Exotic	Annual	Ornamental	Yellow	
<i>Tanacetum parthenium</i>	0	0	0	7	Exotic	Perennial	Weedy	White	Radial
<i>Taraxacum officinale*</i>	5	56	23	56	Exotic	Perennial	Weedy	Yellow	Radial
<i>Thymus vulgaris</i>	2	2	1	14	Exotic	Perennial	Weedy	White	Bilateral
<i>Torenia fournieri</i>	0	0	0	1	Exotic	Annual	Ornamental		Bilateral
<i>Tradescantia</i>	3	8	2	6	Native	Perennial	Ornamental	Purple	Radial
<i>Trifolium pratense*</i>	9	20	7	17	Exotic	Perennial	Weedy	White	Bilateral
<i>Trifolium repens</i>	12	122	39	56	Exotic	Perennial	Weedy	White	Bilateral

<i>Verbena</i>	0	0	0	5	Native	Annual	Ornamental		Radial
<i>Veronica</i>	3	8	2	5	Exotic	Annual	Ornamental	Purple	Bilateral
<i>Viburnum dentatum</i>	0	0	0	1	Native	Perennial		White	Radial
<i>Viola</i>	1	1	1	18			Ornamental		Bilateral
<i>Yucca smalliana</i>	0	0	0	3	Exotic	Perennial	Ornamental	White	Radial
<i>Zantedeschia aethiopica</i>	0	0	0	3	Exotic	Annual	Ornamental	White	Radial
<i>Zinnia</i>	2	2	2	14	Exotic	Annual	Ornamental		Radial

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Appendix 2. Complete plant-pollinator network showing interactions between pollinators (right bars) and plants (left bars). Plants are not labeled to species to maintain clarity, but those species categorized as attractive from least-squares regression are shaded in green.



Appendix 3. Pollinators recorded on neighborhood blocks.  $d'$  is floral specialization index from weighted network, described in methods, ranging from less specialized (0) to more specialized (1). Degree is the number of plant species visited by a pollinator morpho-types.

Pollinator	$d'$	Total recorded visits	Degree
<i>Andrena wilkella</i>	0.656	18	11
<i>Anthidium manicatum</i>	0.172	25	13
<i>Agapostemon virescens</i>	0.492	87	23
<i>Agapostemon</i>	0.210	19	9
<i>Augochlora pura</i>	0.06	2	2
<i>Apis mellifera</i>	0.298	245	44
<i>Bombus pennsylvanicus</i>	0.285	26	16
<i>B. bimaculatus</i>	0.342	78	29
<i>B. griseocollis</i>	0.294	12	8
<i>B. fervidus</i>	0.264	28	17
<i>B. impatiens</i>	0.338	190	48
<i>Ceratina</i>	0.135	1	1
<i>Coelioxys</i>	0.511	2	1
<i>Halictus ligatus</i>	0.299	25	13
<i>Hylaeus</i>	0.478	231	46
<i>Lasioglossum</i>	0.219	274	63
<i>Megachile</i>	0.297	132	35
<i>Melissodes bimaculata</i>	0.128	36	14
<i>Melissodes</i>	0.257	36	16
<i>Nomada</i>	0.389	9	8
<i>Stelis louisae</i>	0.180	3	2
<i>Syrphus</i>	0	13	11
<i>Toxomerus</i>	0.524	309	43
<i>Xylocopa virginica</i>	0.703	14	9

## **Chapter IV. Influence of top down and bottom up forces on herbivorous insects in urban agriculture**

Submitted to Biological Control with E.S. Minor as co-author

### **Abstract**

Larger, concentrated resource patches are hypothesized to host more abundant herbivore populations. However, top-down forces by natural enemies are another, potentially complementary influence. Herbivore suppression by arthropods is a valuable service for the increasing number of urban food producers that refrain from chemical control of crop pests. We investigated how bottom-up effects from crop patch size and top-down effects from the predator and parasitoid community influenced two herbivorous pests of brassica crops in urban agriculture. We sampled for pests and natural enemies at three levels of urban food production: residential gardens, community gardens, and urban farms. At a subset of community gardens, we analyzed if cultivation in raised beds or at ground-level affected ground-dwelling predators. Herbivore populations were recorded at similar abundance in each level of food production, while several natural enemy taxa including specialist wasps and long-legged flies were most common at farms. We found that abundance of certain natural enemies, particularly parasitoids, was a more important driver of leaf and sap-feeding herbivore populations than biodiversity of natural enemies. Herbivory on brassica tended to be low in farms and gardens, most likely due to the presence of specialized parasitoid families and labor-intensive pest management practices. Cultivation in raised beds caused a reduction in ground-dwelling predator abundance. This study suggests that urban agriculture provides a beneficial habitat for arthropod natural enemies, who in turn can provide regulating ecosystem services such as herbivore suppression to urban farmers.

## Introduction

Herbivores with restricted host ranges are hypothesized to have larger populations in concentrated host-plant patches (Root 1973). This resource concentration hypothesis, a bottom-up force of insect regulation, has been studied extensively. However, the results demonstrate conflicting outcomes, with some studies finding a positive relationship between insect pests and patch area (Kareiva 1985, Bach 1988) and other studies finding negative or neutral effects (Cromartie 1975, Capman et al. 1990, Grez and Gonzalez 1995). Variability in the relationship between pests and patch size has been explained by distance between patches (Capman et al. 1990) and organism-dependent dispersal behavior (Grez and Gonzalez 1995, Hamback and Englund 2005). While the bottom-up approach is a useful framework for understanding pest population patterns, top-down controls by arthropod predators (Walker and Jones 2001, Denno et al. 2002, Costamagna and Landis 2006) are alternate, if not synergistic, explanations for herbivore dynamics.

Diversity of natural enemies, and their individual identities, are thought to be the two main drivers of top-down herbivore regulation (Casula et al. 2006, Snyder et al. 2008). Diverse natural enemy communities include species that differ in prey preference and consumption efficiency. This limits redundancy in host selection and creates functional complementarity. Empirical evidence has demonstrated higher herbivore suppression in functionally diverse arthropod communities (Wilby and Thomas 2002, Snyder et al. 2008). On the other hand, natural enemy identity can be equally important (Chalcraft and Resetarits 2003), especially if only a subset of natural enemies are capable of suppressing a specialized insect pest. The absence of certain efficient natural enemies, especially in the simplified habitats of agroecosystems, affects herbivore populations in food crops (Bianchi et al. 2006). Top-down control could be further

weakened in urban agriculture due to differences in arthropod communities compared to natural areas (McIntyre et al. 2001, Faeth et al. 2011). More work is needed to understand the relationship between biodiversity and ecosystem provisioning in urban agriculture (Lin et al. 2015).

Urban agriculture provides a novel setting to examine the relationship between herbivores, plant patch size, and natural enemies. Although far smaller in acreage than conventional production, urban agriculture alleviates food insecurity (Zezza and Tasciotti 2010), offers aesthetic and public health benefits to residents (Fuller et al. 2007), and provides economic benefit (Grewal and Grewal 2012) such as employment in low-income neighborhoods. Commercial-level urban agriculture can be integrated into urban planning (Lovell 2010) and is being championed as an option for increasing productivity of vacant lots in economically-depressed US neighborhoods (Kaufman and Bailkey 2000). Biological control will be a key component of suppressing insect pests in urban agriculture, as many gardens follow organic practices. Predation reduces pest abundance on urban ornamental shrubs (Shrewsbury and Raupp 2006) and may be important for urban food crops too (Gardiner et al. 2014).

Three scales of urban agriculture exist in North American cities, each with a different goal and intensity of production. First, urban farms focus on commercial sale of crops grown outdoors, in greenhouses, or on rooftops. Second, community gardens are allotment-type gardens (Lin et al. 2015) where food is typically grown in polycultures for personal consumption or commercial sale. Unlike urban farms, which are managed as a single unit, each community garden plot is usually managed independently. Finally, residential gardens, or “home-food gardens” are found at multi- or single-family homes where plants are grown exclusively for personal consumption (Taylor and Lovell 2014). All three scales of agriculture offer insect and

floral resources that support herbivores and natural enemies.

In this study, we examined pests and natural enemies at all three scales of urban agriculture. We focused on pests of the brassica family, which contains many common crops such as cabbage, kale, and broccoli. We asked three questions about predators and prey in this system. First, do bottom-up effects of patch size or top-down effects from natural enemies exhibit a greater influence on brassica pests? Second, is diversity or abundance of key functional natural enemy groups (i.e. predators, parasitoids, specialist parasitoids) related to pest abundance? Third, do natural enemy abundance and community composition differ by scale of agriculture? This work provides foundational data on insects in urban agriculture while building on research that identifies drivers of herbivore populations.

## **Methods**

### *Study sites*

We included 29 sites from three scales of agricultural production: residential gardens (N=12), community gardens (N=9), and urban farms (N=8). Community gardens and urban farms were included if at least 20 brassica plants (range 20-200+) were cultivated in three or more discrete areas such as a >1.5 m row. Residential gardens were included if at least 5 brassica plants were present. At each site, we measured the number of discrete areas, typically cultivated rows, where any crops were planted and the number of areas with brassica crops. We also calculated the total area of planted crops or flowers and the area of tilled soil, which would indicate recent planting. We recorded whether plants were cultivated directly in the ground or in raised beds. We located all sites through posting in a local urban agricultural policy listserv. All sites were located in Chicago, IL, except for one urban farm located in the adjacent suburb of Evanston, IL. Minimum distance between nearest sites averaged 1.9 km (range 0.72 -4.2 km).



### *Sampling for insect pests*

We focused on two important groups of brassica pests. The first group, cabbageworms, includes a complex of 3 specialist herbivore species: cabbage looper (*Trichoplusa ni*), diamondback moth (*Plutella xylostella*), and imported cabbageworm (*Pieris rapae*). Cabbageworm eggs and larvae are commonly parasitized by specialist parasitic wasps (Godin and Boivin 1998, Shelton et al. 2002), but records exist of predation by lacewings, yellow jackets, and other arthropods (Richards 1940, Schmaedick and Shelton 1999). The second group, sap-feeding aphids, primarily includes green peach aphid (*Myzus persicae*) and cabbage aphid (*Brevicoryne brassicae*) and are attacked by a broader range of specialist and generalist predators (White et al. 1995, Snyder et al. 2006).

At each site, we randomly selected five *Brassica oleracea* plants (e.g., cabbage, broccoli, kale) and inspected five leaves on each plant for the presence of aphids and cabbageworm eggs, larvae, and pupae. In the case of compact head cabbages, we inspected the entire visible part of the plant, including the wrapper leaves, instead of pulling off individual leaves. In addition to counting pests, we estimated defoliation on the five selected plants on a 0-100% scale at 10% intervals. As we walked through crop rows, we also recorded the presence of adult cabbageworms in-flight. Cabbageworms were identified to the species level but aphids were not. We sampled for cabbageworms and aphids at six intervals between 16 June and 26 August 2014, counting pests and estimating defoliation every other week. At one residential site, brassica plants grew poorly. Therefore, we excluded this site from analysis of pest populations, resulting in 28 sample sites for pests.

### *Sampling for natural enemies*

We set up four 18x14 cm yellow sticky cards (Alpha Scents: West Linn, OR) within

brassica crops at each farm or garden. Cards remained in the field for two-week intervals and were replaced when we visited sites to record pests. In total, we had 5 two-week intervals of natural enemy sampling. After each sampling period, we brought yellow sticky cards to the lab to identify predators and parasitoids on each card. We identified parasitoid wasps to the family level. Since parasitoids vary in their selection of host insects, we also noted the 18 families of parasitoid wasps known to parasitize the egg, larval, or pupal stages of Lepidoptera, the insect Order that includes cabbage worms (Appendix A). We also noted parasitoids in the Aphidiinae subfamily of Braconidae, which are specialist parasitoids of several aphid species. From here on, we refer to these 19 families as ‘specialist parasitoids’. Additionally, we recorded the abundance of common insect predators that may attack aphids and the immature life stages of cabbageworms. These predators, collected on sticky cards, included lady beetles (Coleoptera: Coccinellidae), minute pirate bugs (Hemiptera: Anthocoridae), predatory wasps (Hymenoptera: Vespidae, Crabronidae), hover flies (Diptera: Syrphidae), long-legged flies (Diptera: Dolichopodidae), and lacewings (Neuroptera). From the parasitoid and insect predator families listed above, we calculated the Shannon diversity index of natural enemy diversity for each site.

In a separate study, at four of the community gardens, we used pitfall traps to evaluate the effect of raised beds on abundance of ground-dwelling arthropod predators (Formicidae, Carabidae, Staphylinidae, Opiliones, Araneae). We placed pitfall traps in 31 raised beds and 7 ground-level beds, each containing brassica plants. As ground-level beds are less common in community gardens, all 7 ground-level beds were in a single community garden. The raised beds, which ranged in height from approximately 0.3 m to 0.7 meter tall, were spread among the four community gardens. We used four pitfall traps per bed, filling each trap with propylene glycol as a preservative and protecting them with rain covers. We replaced pitfall traps bi-weekly over 5

weeks.

### *Data analysis*

We compared the intensity of crop production at each scale of agriculture using one-way ANOVAs to investigate if the number of crop rows, rows with brassica, and total area of crop production differed among farms, community gardens, and residential gardens. The number of crop rows and rows with brassica were log-transformed to improve normality. Additionally, we investigated if the dominant bed type (ground versus raised bed) varied by scale of agriculture using a Chi-square test.

We used Generalized Linear Models (GLMs) to test for the effects of scale of agriculture, sample date, and natural enemy diversity on insect pests. Our response variables included abundance of cabbageworm larvae, adults, aphids, and defoliation. We used Poisson distribution for pests and binomial distribution for defoliation. For each response variable, we tested five different measures of the natural enemy community as predictor variables: parasitoid abundance, predator abundance, specialist parasitoid abundance, total natural enemy abundance, and Shannon diversity per site. Total natural enemy abundance was strongly correlated ( $r=0.97$ ) with parasitoid abundance and was removed from models. For post-hoc comparisons, we used generalized linear hypothesis tests (glht) with Tukey's pairwise comparisons in the multcomp package (Hothorn et al. 2008).

We further investigated how the natural enemy community varied with scale of agriculture and sample date. We used GLMs with a poisson distribution to examine the abundance of all parasitoids, all predators, Shannon diversity of natural enemies, and each predator taxon separately. We also investigated if natural enemy community composition (parasitoid families and insect predators) varied by scale of agriculture using ANOSIM. All

statistical analyses were performed in R 3.1 (R Development Program 2014).

Finally, we used a Kruskal-Wallis test to compare ground-dwelling predator abundance between ground-level and raised beds. This analysis was conducted in two ways. First, we included all data in the Kruskal-Wallis test (31 raised beds and 7 ground-level beds). Second, to account for the uneven sample design and the uneven spatial distribution of beds, we also tested the subset of data collected from the garden with ground-level beds (7 raised beds and 7 ground-level beds).

## **Results**

### *Food production in urban agriculture*

Across all study sites, 42% of cultivated rows were dedicated to brassica. Cabbage and kale were the most common cultivars of brassica in this study. Farms and community gardens had significantly more crop rows ( $F=13.94$ ,  $P<0.001$ ) and rows with brassica ( $F=14.50$ ,  $P<0.001$ ) than residential gardens (Table 1). This pattern differed slightly for area of food production, as farms had the greatest food production area compared to both other scales of agriculture ( $F=13.82$ ,  $P<0.001$ ). We identified a non-significant trend toward growing crops in raised beds at community gardens and in the ground at urban farms ( $\chi^2=4.74$ ,  $P=0.10$ ).

### *Pests in brassica*

On average ( $\pm$ SE),  $4.1 \pm 0.6$  eggs,  $1.7 \pm 0.3$  larvae, and  $0.3 \pm 0.1$  pupae of cabbageworms were found on five brassica plants per site. Over 70% of immature cabbageworms were imported cabbageworm (ICW), and nearly all of the remaining immature cabbageworms were cabbage looper. Few cabbage looper and diamondback moth adults were recorded. Consequently, most of our results on cabbageworms are applicable primarily to ICW. On average,  $27.1 \pm 8.2$  aphids were recorded per brassica plant. Mean defoliation was 10.4% of each leaf.

The GLMs revealed a significant effect of date on cabbageworm larvae (Table 2) with discrete population peaks at the 30 June sample date and the 28 July and 11 August sample dates (Fig. 1). In addition to the significant effect of sample date, cabbageworm larvae were significantly affected by total parasitoid and specialist parasitoid abundance (Table 2). Significantly fewer adult cabbageworms were found in residential gardens than community gardens and urban farms ( $z=3.74$ ,  $P<0.01$ , Fig. 1). Adult cabbageworms were also marginally affected by abundance of specialist parasitoids and Shannon diversity of natural enemies. While there was no overall effect of scale on aphid abundance, there were significant effects of total parasitoid and specialist parasitoid abundance. Mean aphid abundance was 2x greater on August 11 and 26 higher compared to any previous sample date, but this was driven by a small number of sample locations and was not statistically significant. Defoliation was not explained by any of the predictor variables (Table 2).

#### *Natural enemies in brassica*

As a group, parasitoid wasps were much more abundant than insect predators (Appendix A). We identified parasitoids from 29 families. Braconidae and Ichneumonidae were the most abundant families. Only two families were phytophagous, Cynipidae and Tanaostigmatidae, but they were recorded infrequently. Of the insect predators recorded on sticky cards, long-legged flies and predatory wasps were the most abundant taxa (Appendix B).

We found a significant effect of date on all natural enemy groups (Table 3, Supplementary Material Appendix C), most of which were more abundant at later sampling dates. The exceptions were Syrphidae ( $z=3.06$ ,  $P=0.02$ ) and Dolichopodidae ( $z=3.43$ ,  $P<0.01$ ), which were most abundant in late June. Although there was a trend towards greater parasitoid abundance at urban farms (Fig. 2), this was only significant for specialist parasitoids of

cabbageworms ( $z=2.89$ ,  $P=0.01$ ). Long-legged flies were more abundant at urban farms compared to residential gardens (Appendices B and C), while the opposite pattern was present for minute pirate bug and for Shannon diversity of all natural enemies. No other natural enemy taxa differed in abundance by scale of agriculture. The ANOSIM indicated no significant difference in natural enemy community composition by scale of food production ( $R=0.04$ ,  $P=0.20$ ).

At community gardens, raised beds had significantly fewer ground-dwelling predators (mean=7) compared to ground-level beds (mean=24,  $\chi^2=21.3$ ,  $P<0.01$ ). This held true even when only examining the single garden with both raised and ground-level beds ( $\chi^2=9.8$ ,  $P<0.01$ ). Harvestmen and spiders were the most common taxa in pitfall traps (Appendix D)

## **Discussion**

Our study revealed the presence of insect herbivores and a diverse natural enemy community at all three scales of urban agriculture. We found few differences between each scale of agriculture in terms of the pest and natural enemy community. Abundance of cabbageworm larvae and aphids—two important pests of brassica crops—was explained by parasitoid abundance but not by scale of agriculture. These results provide support for top-down control of insect pests rather than the resource concentration hypothesis. Other work in urban systems also supports the importance of top-down effects on herbivores by arthropod predators (Shrewsbury and Raupp 2006; but see Raupp et al. 2001) as well as avian predators (Marussich and Faeth 2009).

Of all insect pests, only adult cabbageworms differed in abundance between the three scales of agriculture. Adults were significantly more abundant in urban farms compared to community and residential gardens. At this life stage, cabbageworm butterflies feed on nectar

and prefer to visit larger gardens with more flowers (Matteson and Langellotto 2012). Additionally, ICW, the most abundant cabbageworm species in this study, prefers flowers with high amino acid content (Alm et al. 1990), which may be more common in areas with diverse floral resources. Since adult cabbageworms have long dispersal distances (Jones et al. 1980, Talekar and Shelton 1993), they may readily move around the urban landscape in search of oviposition sites in vegetable gardens. Although the number of eggs laid by ICW is unrelated to patch size (Fahrig and Paloheimo 1987), adults might be expected to locate suitable egg-laying sites more rapidly in farms. However, cabbageworm larvae and aphid abundance were similar at each agricultural scale and unrelated to brassica production intensity. Our results for both crop pests are consistent with the findings of Grez and Gonzalez (1995), who also noted that densities of cabbageworm larvae and aphids did not vary significantly among brassica patches that were comparable in size to our three urban agriculture scales.

Compared to larger non-urban farms, we recorded fewer aphids and cabbageworms per plant (Root 1973, Grez and Gonzalez 1995) and reduced damage to brassica heads or foliage (Shelton et al. 1982, Maltais et al. 1998). We attribute this to several characteristics that are unique to urban agriculture. First, community gardens and farms experience strong volunteerism, information sharing, and neighborhood engagement that results in near daily management (Holland 2004, Barthel et al. 2010). Volunteers perform tasks including weeding and hand-picking pests off plants, a component that most sampled sites included in their organic pest management practices (personal communication with DML). Therefore, most cabbageworms would be noticed shortly after hatching and destroyed before defoliating plants. Second, the small size of urban farms— the largest in Chicago, IL is 2.8 ha – could be insufficient to host large cabbageworm populations. As ‘island habitats’ in an urban matrix, vegetable production is

a small percentage of urban land cover and distributed unevenly between neighborhoods (Taylor and Lovell 2012). Thus, the immigration rate from larger, rural brassica patches would be reduced.

Most natural enemy taxa did not differ in abundance by scale of agriculture. The natural enemy community was dominated by a small number of families that were present at most sites. Four parasitoid families and two predator families comprised 76% and 62% of the parasitoid and predator samples, respectively. The dominance of these families likely explains the fact that community composition was similar at each food production scale. Parasitoid families such as Braconidae and Pteromalidae are common in cities (Bennett and Gratton 2012) due to their broad host range on multiple insect Orders and the presence of diverse hosts in urban agriculture. Many predators in urban agriculture are also generalists (Gardiner et al. 2014), and they can compensate for low cabbageworm abundance by locating alternate prey on other crops. In addition to insect hosts, flowering ornamental plants, present around the edges of all sites and sometimes within crop rows, are a suitable resource for predators including lacewings (Jacometti et al. 2010), hover flies (White et al. 1995), and long-legged flies (Ulrich 2004). Extensive cultivation of ornamental plants in residential neighborhoods (Smith et al. 2006) extends the flowering season in cities, providing natural enemies with ample opportunities to supplement their diet near gardens. In addition to resources from ornamental plants and food crops, urban food production provides microclimates of different temperatures and shading. As a result, urban agriculture may be a preferred habitat for natural enemies compared to turf-grass dominated areas.

Nonetheless, abundance of a few natural enemy groups differed between the three agricultural scales. Farms hosted more specialist parasitoids of cabbageworms than residential



gardens. Although the parasitoids' hosts were not more abundant at farms, long-term brassica cultivation at farms may result in overwintering parasitoid colonies that use host-induced plant volatiles for locating a restricted group of pests (Puente et al. 2008). We found the opposite pattern for minute pirate bugs, which were most abundant in residential gardens. *Orius insidiosus*, the sole recorded species of minute pirate bug, is a predator of soybean aphid (Rutledge et al. 2005), a pest that overwinters on buckthorn and uses legumes and clover as secondary hosts (Ragsdale et al. 2004). These non-crop plants are likely more common in residential properties, perhaps explaining the distribution of pirate bugs. Differences in some natural enemy taxa between agricultural scales would explain the marginal reduction of Shannon diversity at urban farms.

Strong seasonality was evident for natural enemies and pests. These patterns were fairly consistent among the three scales of urban agriculture. Aphids and natural enemies were most abundant at the end of August, while cabbageworm larvae experienced a first peak at the end of June and a second peak about a month later. The increase in natural enemies toward the end of the season could result in several pathways of intraguild predation (Straub et al. 2008), dampening the effects of top-down control by predators on brassica pests.

Within-garden cultivation practices affected ground-dwelling predators. In this study, ground-dwelling predators were nearly absent in raised beds, potentially due to variable management practices by different gardeners, soil matter content (Grewal et al. 2011), and height barriers (Snyder and Wise 1999). Other studies of below-ground predators and biocontrol in vacant lots and community gardens (Yadav et al. 2012, Gardiner et al. 2014) demonstrate that local characteristics influence below-ground predator activity. Since raised beds are more common at community gardens, the predator community's effect on root and foliar herbivores

may differ across agricultural scale. The implications for raised-bed cultivation of crops whose insect pests are controlled by spiders and other soil-dwelling predators warrant further investigation.

We acknowledge several limitations to this study. While parasitoids were the most abundant natural enemy group, sampling by sticky cards rather than foliar counts or sweep sampling underestimates generalist predator populations (Schmidt et al. 2008). Daytime sampling of cabbageworms reduces the potential for recording nocturnal diamondback moth and cabbage looper adults. However, the dominance of ICW in egg and larva counts suggested that other cabbageworm species are secondary pests. Finally, we were unable to control the brassica cultivars between sites due to the high number of gardeners and annual turnover in management of community garden plots. Cabbageworm abundance and parasitism can differ by *B. oleracea* cultivars and leaf structure (Pimentel 1961, Godin and Boivin 1998).

Our study suggests that urban agriculture provides valuable habitat for natural enemies, which influence pest populations through top-down control. Abundant specialist parasitoids resulted in low cabbageworm and aphid abundance during most sampling events. Top-down control of herbivores occurs in both structurally complex natural systems (Langellotto and Denno 2004) and agro-ecosystems (Costamagna and Landis 2006). Since urban agriculture is a structurally complex agro-ecosystem, it is reasonable for top-down control to be a dominant force at this small-scale. Though urban agriculture is a limited land use in cities, its resources, habitats, and growing substrates add diversity to an area dominated by impervious surface and turf grass. Low rates of defoliation and a diverse natural enemy community at all food production scales offer a positive outlook for crop productivity in urban agriculture.

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## TABLES

Table 1. Mean food and brassica production at each scale of urban agriculture. Differences in letters indicates significant post-hoc differences in food production intensity.

	Community garden	Urban farm	Residential garden
Number of crop rows ( $\pm$ SE)	28.0 $\pm$ 6.7 <sup>A</sup>	35.4 $\pm$ 10.4 <sup>A</sup>	5.4 $\pm$ 2.1 <sup>B</sup>
Number of brassica rows ( $\pm$ SE)	13.9 $\pm$ 4.5 <sup>A</sup>	8.1 $\pm$ 1.9 <sup>A</sup>	1.4 $\pm$ 0.18 <sup>B</sup>
Food production area ( $\pm$ SE) m <sup>2</sup>	266 $\pm$ 71 <sup>B</sup>	2088 $\pm$ 611 <sup>A</sup>	22.3 $\pm$ 3 <sup>B</sup>
% of garden beds that were raised	77	25	50



Table 2. Results from GLM to determine effects of scale of agriculture, date, and natural enemies on brassica pests and defoliation.

Each cell contains the F value for the predictor variable in the column heading. For significant F values, we use the following notation:

# $P \leq 0.10$ , \* $P \leq 0.05$ , \*\* $P \leq 0.01$ . Pseudo  $R^2$  [ $1 - (\text{Residual}/\text{Null deviance})$ ] is presented for the reduced model that only contains the significant terms.

Response variable	Scale	Date	Scale x Date	Parasitoids	Specialist parasitoids	Predators	Shannon diversity	Pseudo $R^2$
CW Larva	0.69	5.17**	0.57	4.07*	5.34*	0.67	0.12	0.34
CW Adult	3.07*	0.44	1.77#	0.36	2.82#	0.05	3.22#	0.32
Aphid	0.80	1.62	0.16	8.64**	3.78*	0.05	2.73	0.38
Defoliation	0.70	1.08	0.97	0.66	0.57	0.01	0.05	0

Table 3. Results from GLM to determine effects of scale of agriculture and date on common natural enemy groups. Each cell contains the F value for the predictor variable in the column heading. For significant F values, we use the following notation: \* $<0.05$ , \*\* $<0.01$ . Pseudo  $R^2$  [1 – (Residual/Null deviance)] is presented for the reduced model that only contains the significant terms.

Natural enemy	Scale	Date	Scale x Date	Pseudo $R^2$
All parasitoids	2.06	12.74**	0.30	0.43
Cabbageworm	13.27**	7.75**	1.17	0.37
parasitoids				
Aphid parasitoids	1.53	15.62*	0.59	0.58
Predators	0.12	5.16**	0.42	0.18
Shannon diversity	3.54*	6.81**	0.44	0.21

## FIGURES

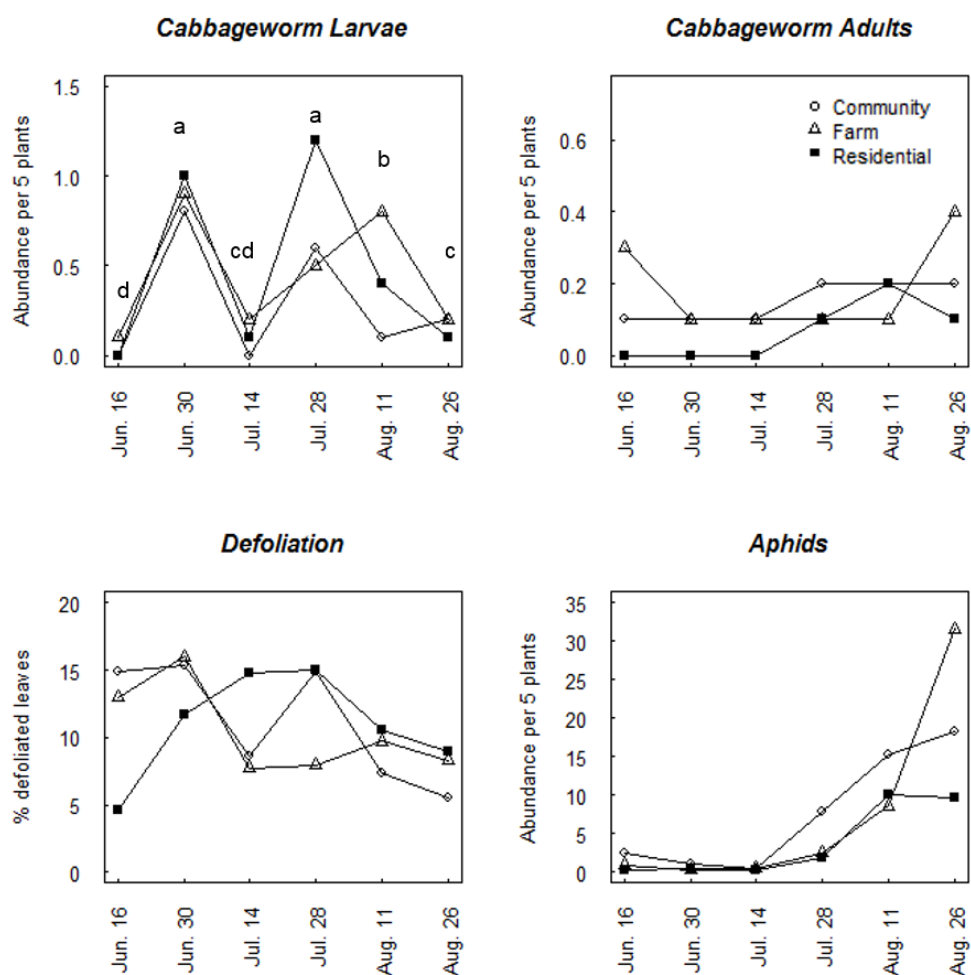


Figure 1. Mean cabbageworm larva, adult, and aphid abundance, and defoliation, across the six sample dates. For cabbageworm larvae, differences in lower case letters indicate significant post-hoc differences by sample date.

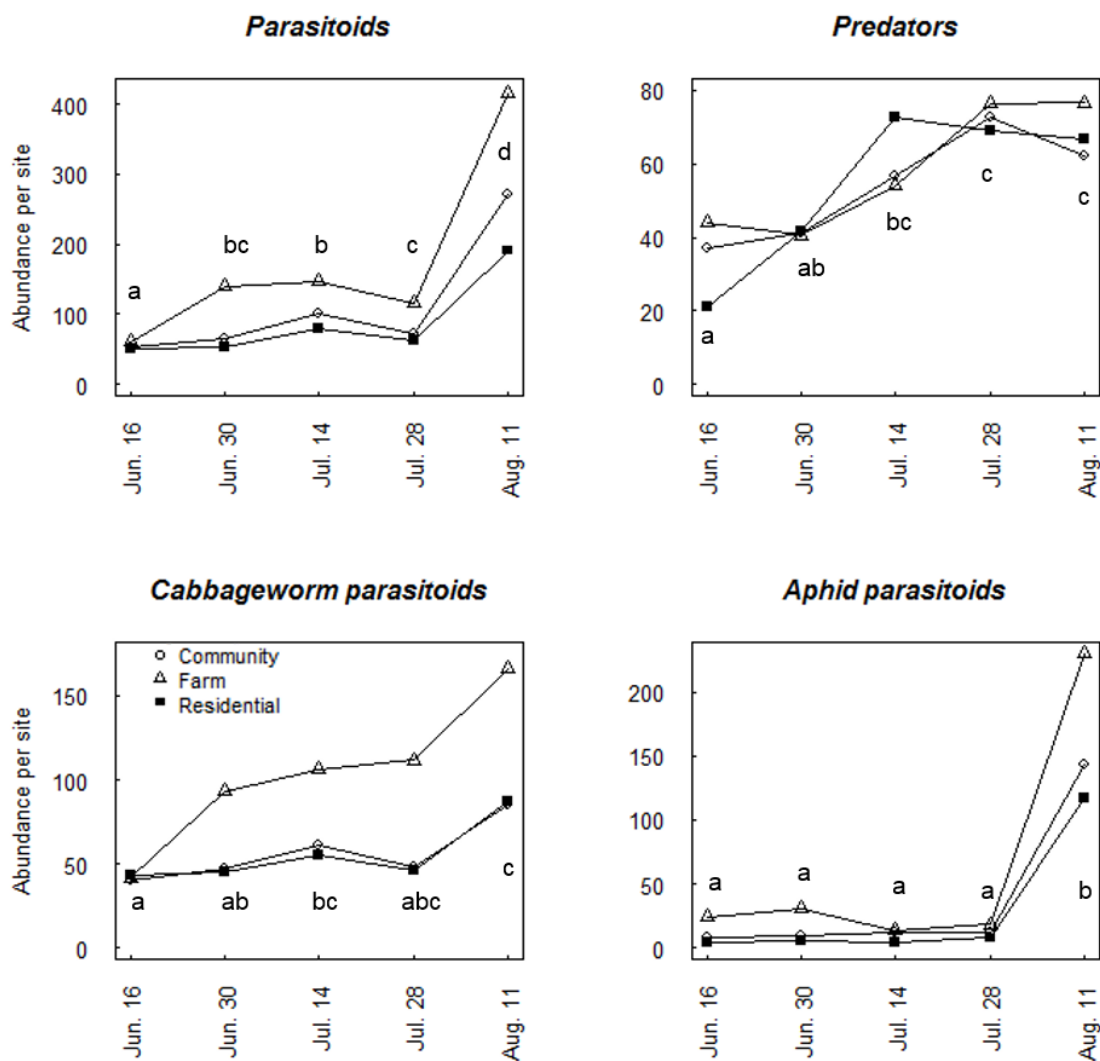


Figure 2. Mean natural enemy abundance on yellow sticky cards at the three scales of agriculture.

Sample date is the start of 2-week period when sticky cards were left in each garden.

Cabbageworm parasitoids include the 18 families known to attack Lepidoptera. Aphid parasitoids are specialists from the Aphidiinae subfamily. Differences in lower case letters indicate significant post-hoc differences by sample date.

## APPENDICES

Appendix A. Abundance of parasitoid wasps and insect natural enemies recorded on yellow sticky cards. Families are listed in order of total abundance. Percentages are calculated separately for parasitoids and insect predators.

Natural enemies	Total abundance	Percent of total abundance
<b>Parasitoid wasps</b>	20550	
Braconidae specializing on aphids (Aphidiinae)	5844	28.44
Ichneumonidae*	4805	23.38
Pteromalidae*	2739	13.33
Eucoilidae	2269	11.04
Braconidae not specializing on aphids*	1669	8.12
Diapriidae*	834	4.06
Platygastridae	531	2.58
Eulophidae*	337	1.64
Mymaridae*	333	1.62
Ceraphronidae	324	1.58
Encyrtidae*	208	1.01
Trichogrammatidae*	86	0.42
Chrysididae	83	0.40
Cynipidae	73	0.36
Pompilidae	69	0.34
Perilampidae*	61	0.30
Scelionidae*	55	0.27
Eupelmidae*	52	0.25
Aphelinidae	42	0.20
Megaspilidae	39	0.19
Eurytomidae*	32	0.16
Proctotrupidae	28	0.14
Eucharitidae	11	0.05
Tiphiidae	9	0.04
Tanaostigmatidae*	4	0.02
Torymidae	4	0.02
Signiphoridae*	3	0.01
Bethylidae*	2	0.01
Chalcididae*	2	0.01
Figitidae	2	0.01
<b>Insect predators</b>	7720	

Dolichopodidae (Long-legged flies)	2526	32.72
Vespidae (Predatory wasps)	2285	29.59
Anthocoridae (Minute pirate bugs) <sup>b</sup>	953	12.34
Formicidae (Ants)	883	11.44
Coccinellidae (Lady beetles) <sup>a</sup>	586	7.59
Neuroptera (Lacewings)	222	2.88
Syrphidae (Hover flies)	265	3.43
Crabronidae (Predatory wasps)	50	0.01

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\* Indicates that wasp family is classified as a ‘specialist’ capable of parasitizing insects in the Order Lepidoptera.

<sup>a</sup> Includes the following species: *Coccinella septumpunctata*, *Coleomegilla maculata*, *Harmonia axyridis*, *Hippodamia convergens*, and *Propylea quatuordecimpunctata*.

<sup>b</sup> This family consisted of 1 species- *Orius insidiosus*

Appendix B. Mean number of individuals in each predator taxon ( $\pm$  SE) per four sticky cards at each site. Letters after each value indicate significant differences identified by Tukey's posthoc tests using the multcomp library in R.

Natural enemy	Community garden	Urban farm	Residential garden
Long-legged fly	20.19 $\pm$ 3.15 <sup>AB</sup>	22.87 $\pm$ 4.97 <sup>A</sup>	13.2 $\pm$ 1.91 <sup>B</sup>
Predatory wasp	14.95 $\pm$ 2.31	17.97 $\pm$ 2.84	16.55 $\pm$ 3.31
Lady beetle	4.70 $\pm$ 0.73	5.03 $\pm$ 1.38	3.24 $\pm$ 1.04
Lacewing	1.23 $\pm$ 0.33	1.62 $\pm$ 0.85	1.83 $\pm$ 0.61
Hover fly	2.28 $\pm$ 0.47	1.74 $\pm$ 0.47	2.17 $\pm$ 1.08
Minute pirate bug	6.02 $\pm$ 1.70 <sup>AB</sup>	3.59 $\pm$ 0.87 <sup>A</sup>	9.55 $\pm$ 3.67 <sup>B</sup>

Appendix C. Table of GLM results for predator groups. Each cell contains the F value for the predictor variable in the column heading. For values where F is significant, we use the following notation: #<0.10, \*<0.05, \*\*<0.01. Pseudo R<sup>2</sup> [1 – (Residual/Null deviance)] is presented for the reduced model that only contains the significant terms.

Natural enemy	Scale	Date	Scale x Date	Pseudo R <sup>2</sup>
Hover fly	0.18	3.88*	0.47	0.14
Lacewing	0.44	6.83**	0.94	0.28
Lady beetle	1.45	5.11**	0.44	0.22
Long-legged fly	3.72*	2.83*	0.46	0.16
Minute pirate bug	2.47#	5.92**	0.74	0.36
Predatory wasp	0.62	24.60**	0.31	0.56



Appendix D. Ground-dwelling predators collected in pitfall traps listed in order of abundance.

Predator	Abundance
Opiliones (Harvestmen)	186
Lycosidae*	49
Formicidae (Ants)	35
Carabidae (Ground beetles)	24
Dysderidae*	7
Agelinidae*	7
Salticidae*	3
Thomisidae*	3
Linyphiidae*	2
Staphylinidae (Rove beetles)	2
Corinnidae*	1

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\* Indicates families of spiders

## **Chapter V. Substantial mortality of cabbage looper from predators in urban agriculture is not influenced by scale of production or variation in local and landscape-level factors**

### **Abstract**

As Midwestern (USA) cities experience population decline, there is growing interest in converting underutilized vacant spaces to agricultural production. Urban agriculture varies in area and scope, yet most growers use similar cultivation practices such as avoiding chemical control of crop pests. For community gardens and farms that sell produce commercially, effective pest suppression by natural enemies is important for both societal, economic, and marketing reasons. To gauge the amount of predation and parasitism at 28 urban food-production sites, we measured removal of sentinel eggs and larvae of the cabbage looper *Trichoplusia ni* (Hubner), a caterpillar pest that defoliates brassica. We investigated how landscape and local factors, such as scale of production, influence cabbage looper mortality caused by predators. Predators removed 50% of eggs and 25% of larvae over a 3-day period. Landscape factors did not predict mortality rates, and the amount of loss and damage to sentinel prey were similar across sites that differed in scale (residential gardens, community gardens, and farms). To confirm that removal of sentinel items was likely caused by natural enemies, we set up a laboratory assay that measured predation of cabbage looper eggs and larvae by several predators occurring in urban gardens. Lady beetles caused the highest mortality rates, suggesting their potential value for biocontrol; spiders and pirate bugs also consumed both eggs and larvae at high rates. Our results suggest that urban growers benefit from high consumption rates of cabbage looper eggs and larvae by natural enemies.

### **Introduction**

Loss of industry and population decline have resulted in a high number of vacant lots in cities. Recently there has been growing interest in transforming blighted sites into green spaces, such as urban agriculture, with ecologically and economically productive uses (Alig et al. 2004,

Shetty and Reid 2013). Urban agriculture helps reduce food insecurity in low-income communities (Morland et al. 2002, Blaine et al. 2010), provides psychological benefits through increasing green space (Fuller et al. 2007), and offers job training and career skills to low-income populations. While large-scale rural agriculture is often associated with landscape simplification, urban agriculture increases structural complexity through the addition of novel habitats in a system dominated by impervious surfaces. As food production for both home and commercial purposes becomes integrated into the urban landscape (Grewal and Grewal 2011, Taylor and Lovell 2012), there is a need to examine the relationships between biological control of important pests and the scale of production, landscape features, and local site factors.

Chemical inputs offer effective control against many crop pest species but have limited feasibility in cities due to risks of insecticide application in populated areas (Robbins et al. 2001) and due to growers preferring cultural and biological controls. Therefore, natural enemies are a crucial component of prey suppression in urban agriculture. To conserve natural enemies, there must be perennial insect and floral resources as well as suitable habitat (Isaacs et al. 2009). These local-level factors, such as floral diversity, can enhance natural enemy abundance (Fiedler and Landis 2007, Bennett and Gratton 2012a). Polycultures and ornamental plantings in farms and community gardens contribute to diverse parasitoid and predator populations (Gardiner et al. 2014, Lowenstein and Minor in review). Several studies also report an influence of landscape-level factors such as herbaceous cover and forested areas on prey suppression (Werling et al. 2011, Bennett and Gratton 2012b). These landscape measurements, often taken at broader resolution, offer useful comparisons of arthropod populations across an urban-rural gradient (e.g. Bennett and Gratton 2012a) but do not adequately capture fine-scale heterogeneity in land cover or resources at the neighborhood scale (Cadenasso et al. 2007, Lowenstein and Minor 2016). Minimal broad-scale structure in urban landscapes decreases the explanatory power of landscape variables on predators

(Sattler et al. 2010) and could make micro-climates and local-level factors better suited to explain patterns of prey suppression in crop boundaries.

Natural enemies are present in cities and urban agriculture (Bennett and Gratton 2012a, Gardiner et al. 2014, Lowenstein and Minor in review), and it is expected that they will contribute to prey suppression of multiple pest species. Two studies have documented pest control by foliar and ground-dwelling predators in urban agriculture (Yadav et al. 2012, Gardiner et al. 2014). Both studies used sentinel items to evaluate prey suppression but selected species that pose a minimal risk to crop productivity. However, prey suppression may vary between crop families and by natural enemy foraging patterns. Urban growers would benefit from an assessment of the potential for prey suppression in economically important pests that specialize on a single plant group or family. One of these families is the Brassicaceae, which includes cole crops such as cabbage and kale. Brassica experience herbivory from a group of insect pests (Root 1973) that includes three larval species - imported cabbageworm *Pieris rapae* (L.), cabbage looper, and diamondback moth *Plutella xylostella* (L.). In addition to variation in biocontrol between crop families and insect herbivores, the extent of prey suppression may differ by the scale of urban agriculture (Lin et al. 2015) due to variation in habitat characteristics and management techniques.

The dependence of urban agriculture on biological control provides an opportunity to examine the relationship between prey suppression and local and landscape variables in an emerging area of food production. We investigated the potential for prey suppression of pests using cabbage looper eggs and larvae as sentinel items. In particular, we examined how prey mortality varies across the landscape and between three scales of food production - residential gardens, community gardens, and urban farms. We hypothesized that the higher amount of brassica in urban farms would increase the probability of natural enemies locating sentinel items and lead to greater removal of eggs and larvae at this scale of production. After quantifying prey

mortality at each agricultural scale, we modeled the explanatory power of several local (within-garden) and landscape factors to account for variation in cabbage-looper mortality rate. We anticipated that mortality would be greater in sites with higher floral diversity, and that sites isolated from surrounding green spaces would experience reduced prey suppression. To corroborate that mortality could be attributed to natural enemies, we evaluated the potential for several common generalist arthropod predators to consume cabbage looper eggs and larvae in a simplified lab environment.

## Methods

### *Mortality of sentinel eggs and larvae*

Cabbage looper mortality was measured in 28 urban food production sites in Chicago, IL and Evanston, IL, selected to include three scales of urban agriculture: residential gardens, community gardens, and farms (Fig. 1). Each production scale is described in more detail in Lowenstein and Minor (in review). Sentinel eggs and larvae were obtained from a commercial insectary (Frontier Scientific: Newark, DE). Egg masses had been oviposited onto paper towels, which we then cut into approximately 2 x 2 cm sections of 23-28 eggs each. Larvae were obtained at the 2<sup>nd</sup> instar and reared in a growth chamber (16:8 L:D, 26° C) until 3<sup>rd</sup> instar.

Within brassica rows at each site, we deployed 3 egg masses singly beneath separate platforms that were painted green and elevated 0.5 m above the ground. A fourth egg mass covered by a petri dish that excluded natural enemies served as a control. Before being used as sentinel items, 11 replicates of frozen (-30° C) and unfrozen eggs were exposed to field-collected *Coccinella septempunctata* (L. 1758) (Coleoptera: Coccinellidae) in the laboratory. We found no evidence that freezing affected egg-removal rates ( $F_{1,20} = 1.00$ ,  $P = 0.52$ ). Other research using eggs as sentinel items has confirmed similar rates of predation on frozen and unfrozen eggs (Werling et al. 2011, Gardiner et al. 2014). Therefore, egg masses were frozen to prevent

emergence in the field. Beneath each platform we also deployed 3 larvae covered with a 2-mm mesh bag to prevent escape. An additional larva covered by a petri dish to exclude predators served as a control at each site. Sentinel items remained in the field for 72 hours, after which remaining eggs were counted and each larva was inspected for evidence of predation. Egg disappearance and/or damage was measured Aug. 1 and Aug. 14; larval damage was measured on July 13 and Aug. 14, 2014. All undamaged eggs and larvae were returned to the lab and preserved in a 26° C growth chamber for 1 week to check for the emergence of parasitoids. None emerged. The number of damaged items was pooled over both sampling dates, and we calculated separate mortality indices for eggs and larvae. This index was calculated at each site as the number of sentinel items damaged by natural enemies reduced by the number of damaged sentinel items in the control assays protected from predators. The initial number of eggs was similar across replicates (range: 144-155).

#### *Direct observations of predation on eggs and larvae in the field and the laboratory*

We looked for direct evidence that sentinel items were damaged by arthropod predators by setting up time-lapse cameras (Brinno TLC200 Pro) for 24-hour periods at a subset of sites. We obtained 168 hours of footage.

We also evaluated the extent to which damaged sentinel items could be attributed to predation by exposing them in the laboratory to predators found in urban agricultural systems. Each tested predator was starved for 24 hours before being placed in a petri dish with a moistened cotton roll that contained either a mass of 23-30 eggs or a 3rd instar larva. An untreated control group with a single egg mass or larva was set up to confirm that damage was caused by the predator rather than handling damage or mortality from causes other than predation. After 24 hours we recorded the number of damaged or entirely consumed eggs and the number of damaged larvae.

We tested predation by field-collected ground beetles (Coleoptera: Carabidae), harvestmen (Opiliones), ants (Hymenoptera: Formicidae), and spiders (Aranae: Linyphiidae and Lycosidae); insectary-reared minute pirate bugs (*Orius insidiosus* (Say 1832) and lacewings (Neuroptera: Chrysopidae); and lady beetles [combination of field-collected *Coccinella septempunctata* and purchased *Harmonia axyridis* (Pallas 1773) adults and larvae]. Due to difficulties in collecting certain taxa, we had an uneven number of replicates for each predator.

#### *Measuring landscape and local factors*

Three landscape variables (herbaceous cover, impervious surface and tree cover) were obtained from a 100-m buffer around each site calculated using a classified high resolution (sub-meter) QuikBird satellite image and the Tabulate Area tool in ArcGIS 9.3. Eight local variables (i.e. site characteristics) were measured: floral abundance and diversity on each site because nectar is an alternate resource for some natural enemies and its availability can affect the rate of prey suppression (Blaauw et al. 2012); garden size and crop diversity because they can affect the composition of the natural-enemy community (Gardiner et al. 2014); and predator and parasitoid abundance (measured on each sampling date using yellow sticky cards left at each site for a week). Techniques for measuring these local factors and a description of the natural enemy community can be found in Lowenstein and Minor (in review). A summary of all factors, including the range of values each exhibited, appears in Table 1.

#### *Statistical modeling*

We used one-way ANOVA to evaluate evidence for the impact of production scale on numbers of eggs and larvae damaged. Results were similar using a binomial GLM of proportion damaged (not presented). We also used one-way ANOVA to evaluate the impact of predator type on the rate (arcsine-transformed) of egg damage in the lab trials. Chi-square was used to analyze differences between predators in frequency of predation on larvae in the laboratory experiment.

A more complex modeling approach was utilized to evaluate the impact of landscape and local factors on damage to sentinel items. We used an inferential model-selection approach [MuMIn package (R Core Development package, Barton 2015)] that considered model fit from all possible subsets of all potential explanatory variables (Table 1). We constrained the results of model selection by only considering models with  $\Delta AICc < 2$ . For each variable appearing in this subset of models we calculated Akaike weights, which is a relative measure of the strength for the likelihood of each model. Since egg and larval numbers were count data, we used generalized linear models with family = negative binomial for eggs (corrected for overdispersion better than the Poisson) and family = Poisson for larvae. Prior to model selection we investigated for collinearity using the Variance Inflation Factor (VIF). We removed the factor “impervious surface” from potential models because it had a high VIF (13.1) and was negatively correlated with grass cover ( $r = -0.46$ ,  $P=0.01$ ). Additionally we log-transformed parasitoid abundance to improve residuals. We evaluated model performance using Maximum Likelihood pseudo  $R^2$ ; and also McFadden’s Pseudo  $R^2$ , which is  $1 - (\ln(\text{Likelihood (full model)}) / \ln(\text{Likelihood (intercept only)}))$ .

## Results

### *Rates of egg and larval mortality*

Across all 28 sites,  $55\% \pm 3\%$  (mean  $\pm$  SE) of eggs and  $25\% \pm 4\%$  of larvae were damaged or attacked within three days of exposure. Scale of agriculture had no discernable impact on rates of egg damage ( $F_{2,26} = 1.61$ ,  $P = 0.22$ ) or larval suppression ( $F_{2,26} = 0.17$ ,  $P = 0.85$ ) (Fig. 2). From time lapse cameras and observations, we recorded 12 ants, 4 spiders (Lycosidae), 6 lady beetle adults and 4 lady beetle larvae (*C. maculata* and *C. septumpunctata*) feeding on egg masses.

In the 24-hr lab assays, all predators consumed at least ~40% of the eggs, with lady beetle adults and larvae exhibiting the highest consumption rate (~80%) (Fig. 3). Spiders, lady beetle



adults and pirate bugs consumed a substantial number of larvae (~30 – 50%) whereas ants and lacewings consumed very few or no larvae (Fig. 4).

#### *Modeling landscape and local factors to explain variation in egg and larval mortality*

Each of the selected models with  $\Delta AICc < 2$  accounted for very small amounts of variation in egg or larval mortality (Tables 2, 3). The confidence intervals for the effect of each factor on egg or larval mortality overlapped with zero for 7 variables, indicating a poor fit for these models (Fig. 5). Percent brassica defoliation was the only variable whose 95% CI did not overlap zero (Fig. 5), which reflected a weak negative relationship between number of eggs damaged or removed and the percent brassica defoliation in the garden (Fig. 6).

#### **Discussion**

The rates of egg mortality we observed across an urban landscape were similar to rates observed in brassica growing in rural areas (Pisani Gareau and Shennan 2010), while larval mortality was slightly below rates documented for rural farms (Linkous 2013, Bryant et al. 2014, Garfinkel and Johnson 2015). Furthermore, the negative correlation between egg damage and % brassica defoliation (Fig. 6) suggests that using sentinel eggs was a valid technique for assessing predator biocontrol potential in our gardens (i.e. damage was higher where defoliation was lower, presumably due to higher densities of natural enemies). Our findings suggest that the potential for biocontrol of cabbage looper on brassica by generalist predators in urban gardens and farms is comparable to that in rural fields, which offers a positive outlook for urban growers relying on non-chemical management practices. Our results add to previous findings (Yadav et al. 2012, Gardiner et al. 2014) that reveal the potential of generalist predators to suppress pest populations in urban agriculture.

Parasitoids also are effective at reducing cabbageworm populations (Shelton et al. 2002, Pisani Gareau and Shennan 2010, Linkous 2013), with parasitism rates reaching as high as 70% in

brassica stands (Pisani Gareau and Shennan 2010). The absence of parasitoid emergence from reared sentinel items, and the low explanatory power of parasitoid abundance in our model-selection procedure (Fig. 5), together suggest that parasitoids did not contribute to egg or larval mortality in our study. Several factors may explain the lack of evidence for parasitism. First, low rates of parasitism could have been obscured by subsequent damage due to generalist predators, although this is unlikely to be a major contributing factor since ~50% of the eggs and ~75% of the larvae were undamaged after 3 days, yet they harbored no parasitoids. Secondly, cabbage looper has the lowest parasitism rates of the three cabbageworm species that feed on brassica (Shelton et al. 2002, Pinkous 2013). Thirdly, sentinel items were located on elevated platforms, not on the brassica leaves that can emit volatiles in response to herbivore feeding (Dicke and van Loon 2000). Without these volatiles, parasitoids have limited chemical and olfactory signals for host recognition (Najar-Rodriguez et al. 2015, Ponzio et al. 2016).

Our video footage, occasional observations in the field, and laboratory assays suggest that damage to sentinel eggs and/or larvae was due to an array of generalist predators: lady beetle adults and larvae, pirate bugs, harvestmen, spiders (especially Lycosidae, but also Linyphiidae), lacewings, carabid beetles and ants. Other generalist predators, including syrphid fly larvae and yellow jacket wasps, also have been documented to consume cabbageworms (Richards 1940, Bryant et al. 2014). It then may seem surprising that predator abundance performed poorly in our modeling of local factors. One possibility is that the diverse assemblage of generalist predators in urban brassica (Lowenstein and Minor in review), acting as a unit, suppresses prey to such an extent that there is insufficient variation between gardens in the overall effectiveness of this assemblage to detect strong relationships with prey mortality. We acknowledge that the absence of identifying predators to the species level overlooks the effects of species identity and the assemblage of competing predators on cabbageworm predation (Moreno et al. 2010). An

additional explanation, one that is quite likely to be important, is that yellow sticky traps, although effective in sampling parasitoids, are not the best way to sample activity-densities of several of the generalist predators that preyed upon the sentinel items.

Our modeling of landscape and local site variables did not uncover convincing evidence of causal relationships with egg or larval mortality. The only relationship to emerge from the model-selection process was the negative correlation between percent brassica defoliation and egg damage – which was not evidence of causation but simply a correlation between two variables likely related to activity-densities of generalist predators. The result of our modeling effort was surprising, as habitat patterns such as the amount of open space and vegetation characteristics are known to influence population densities of spiders and lady beetles (Magura et al. 2010, Gardiner et al. 2014), the most effective predators of cabbage looper in this study. Furthermore, floral resources appear in the diet of many natural enemies (Isaacs et al. 2009) and are associated with variation in natural enemy diversity in rural farms (Fiedler and Landis 2007, Blaauw and Isaacs 2012). However, flowers are distributed broadly in neighborhoods and gardens in Chicago (Lowenstein and Minor 2016), which supports our finding that variation in floral resources across our 28 sites was not related to cabbage looper mortality. More broadly, our results support the emerging generalization that in intensively managed and disturbed urban areas, variation in prey suppression is largely independent of variation in land-cover features (Fenoglio et al. 2009, Bennett and Gratton 2012b) or local-level vegetation characteristics (Hanks and Denno 1993, Dale and Frank 2014). Our results also suggest that the assemblage of generalist predators is capable of exerting substantial biocontrol of the cabbage looper on brassica grown in backyard plots, community gardens, and commercial farms across a geographically extensive urban landscape.

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## TABLES

Table 1. Landscape and local variables evaluated as explanatory factors for variation in damage to sentinel cabbage looper eggs and larvae.

Variable	Range	Unit	Source
Herbaceous grass cover	6.3-35.7	% cover within 100 m buffer	Quikbird
Impervious surface	5.1-82.5	% cover within 100 m buffer	Quikbird
Tree cover	1.6-68.7	% cover within 100 m buffer	Quikbird
Floral abundance	12-628	Number floral units recorded in entire site	In garden boundaries
Floral richness	1-13	Number flowering plant species recorded in entire site	In garden boundaries
Garden area	15-4421	Meters squared	In garden boundaries
% cropping areas with brassica plants	7-100	%	In garden boundaries
Brassica defoliation	0-20	%	Measured weekly on plant
Parasitoid abundance	90-1855		Measured weekly on yellow sticky cards
Predator abundance	101-742		Measured weekly on yellow sticky cards

Table 2. Summary of top-performing models that explain a portion of the variation in egg damage and have  $\Delta AICc < 2$ . Higher Akaike weights indicate increased model fit.

Model	Coefficients (Beta)	AICc	Akaike weight	Maximum likelihood Pseudo R <sup>2</sup>	McFadden R <sup>2</sup>
Defoliation	B1= -0.02	277.1	0.305	0.11	0.01
Defoliation + Percent brassica	B1= -0.03 B2= 0.37	277.5	0.255	0.18	0.02
Intercept		278.0	0.193		
Defoliation + Percent brassica + Trees	B1= -0.02 B2= 0.44 B3= 0.01	278.7	0.134	0.23	0.03
Parasitoid abundance	B1= 0.34	279.1	0.114	0.05	0.005



Table 3. Summary of top-performing models that explain a portion of the variation in larval damage and have  $\Delta AICc < 2$ . Higher Akaike weights indicate increased model fit.

Model	Coefficients (Beta)	AICc	Akaike weight	Maximum likelihood Pseudo R <sup>2</sup>	McFadden Pseudo R <sup>2</sup>
Grass	B1= -0.04	85.1	0.251	0.11	0.04
Grass + Trees	B1= -0.05 B2= 0.02	85.3	0.228	0.17	0.07
Intercept		86.1	0.159		
Trees	B1= 0.01	86.5	0.125	0.06	0.02
Grass + Floral richness	B1= -0.05 B2= 0.05	86.6	0.123	0.14	0.05
Grass + Floral abundance	B1= -0.05 B2 = 0.001	86.7	0.114	0.13	0.05

## FIGURES

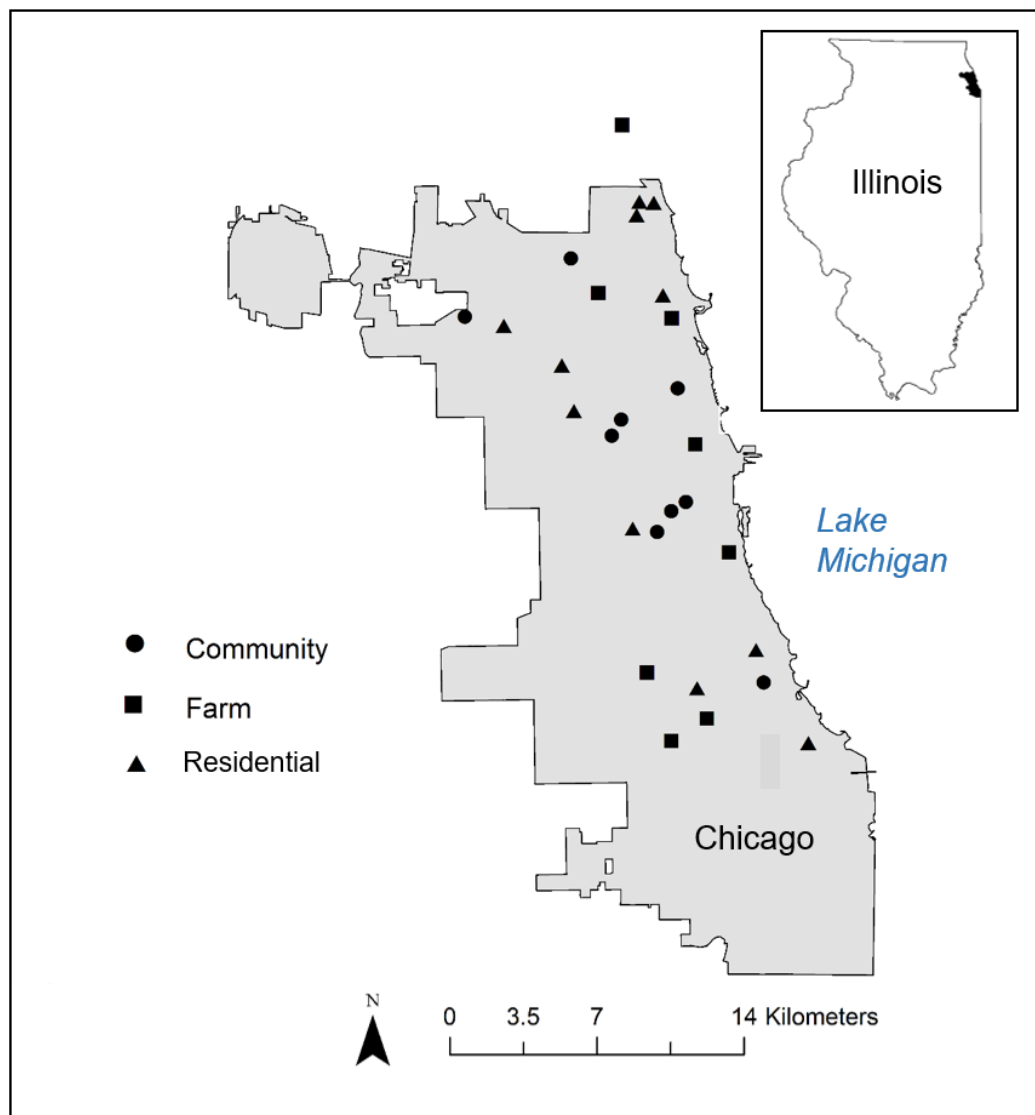


Figure 1. Site locations classified by scale of agriculture in Chicago, IL (grey shading) and Evanston, IL (the farm north of Chicago).

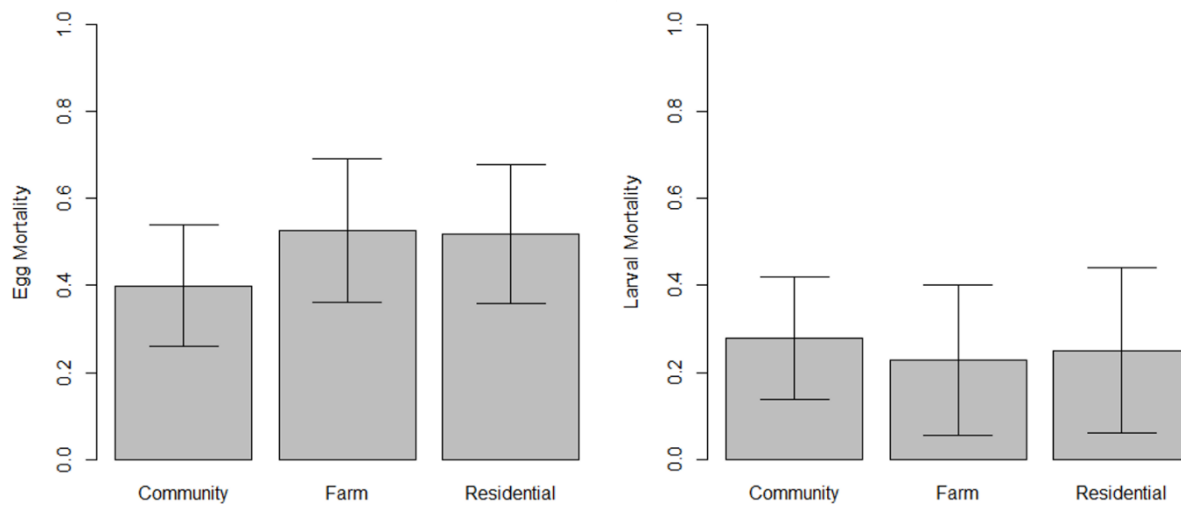


Figure 2. Mean ( $\pm$  95% CI) proportion of sentinel cabbage looper eggs and larvae damaged by predators at each urban agricultural scale.

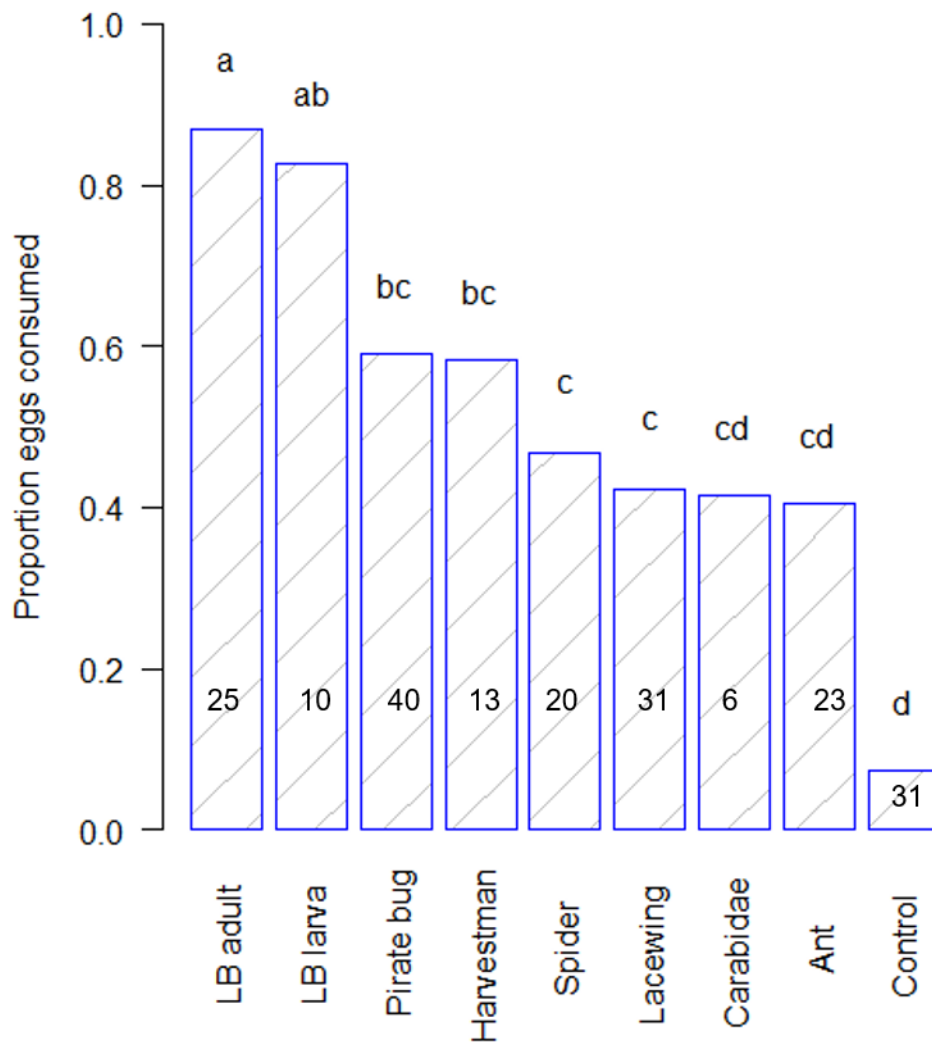


Figure 3. Egg consumption by predators in laboratory assays. Number of replicates is listed within the bar. Each predator replicate was offered an egg mass of 23-28 eggs. Predators differed in consumption rates ( $F_{8, 190} = 17.72$ ,  $P < 0.001$ , one-way ANOVA). Letters above bars indicate differences ( $p < 0.05$ ) based upon Tukey's HSD multiple-comparison test. LB= Lady beetle

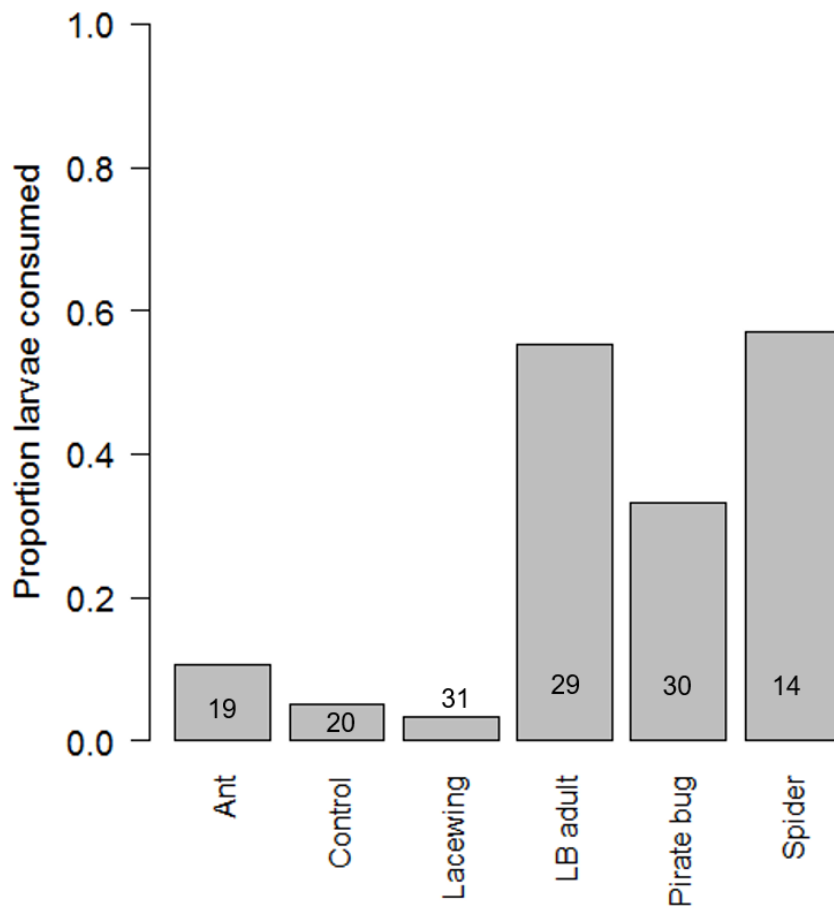


Figure 4. Larval consumption by predators in laboratory assays. Number of replicates within or above the bar. Each predator replicate was offered a single larva. Predators differed in rates of consumption of larvae ( $\text{Chi}^2 = 35.50$ ,  $\text{df} = 5$ ,  $P < 0.001$ ).

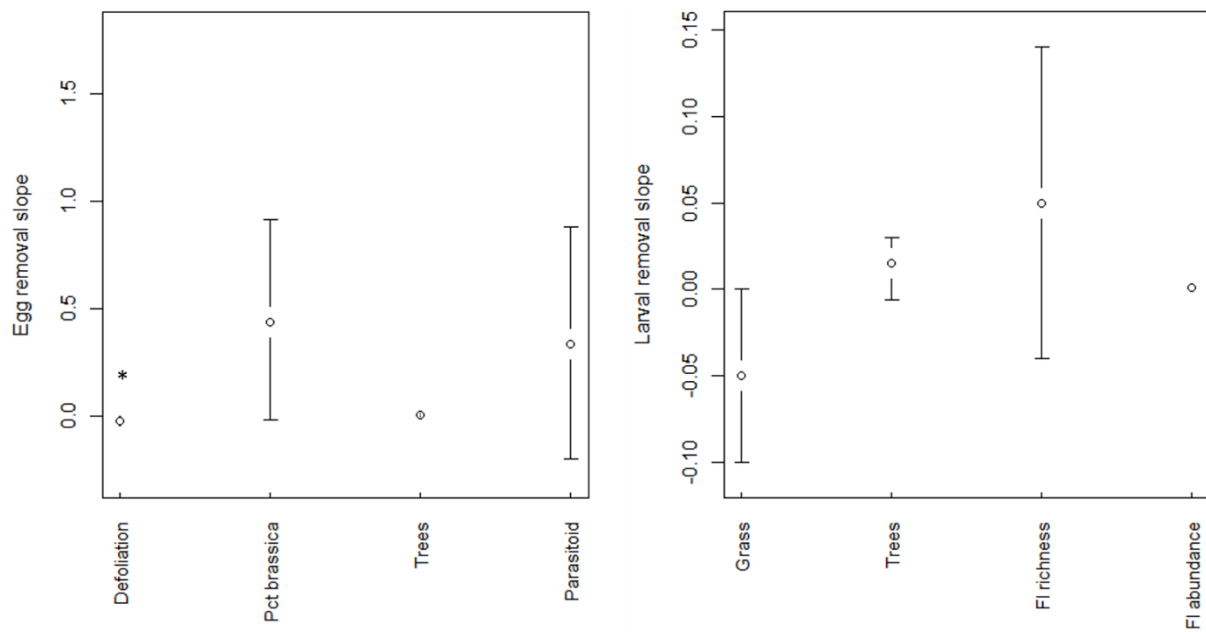


Figure 5. Effect size  $\pm$  95% CI for each predictor variable appearing in candidate models from the model-selection procedure. For variables appearing in multiple models, we used the average of each parameter. Asterisk (\*) indicates that 95% CI does not include zero. Description of variables is presented in Table 1.

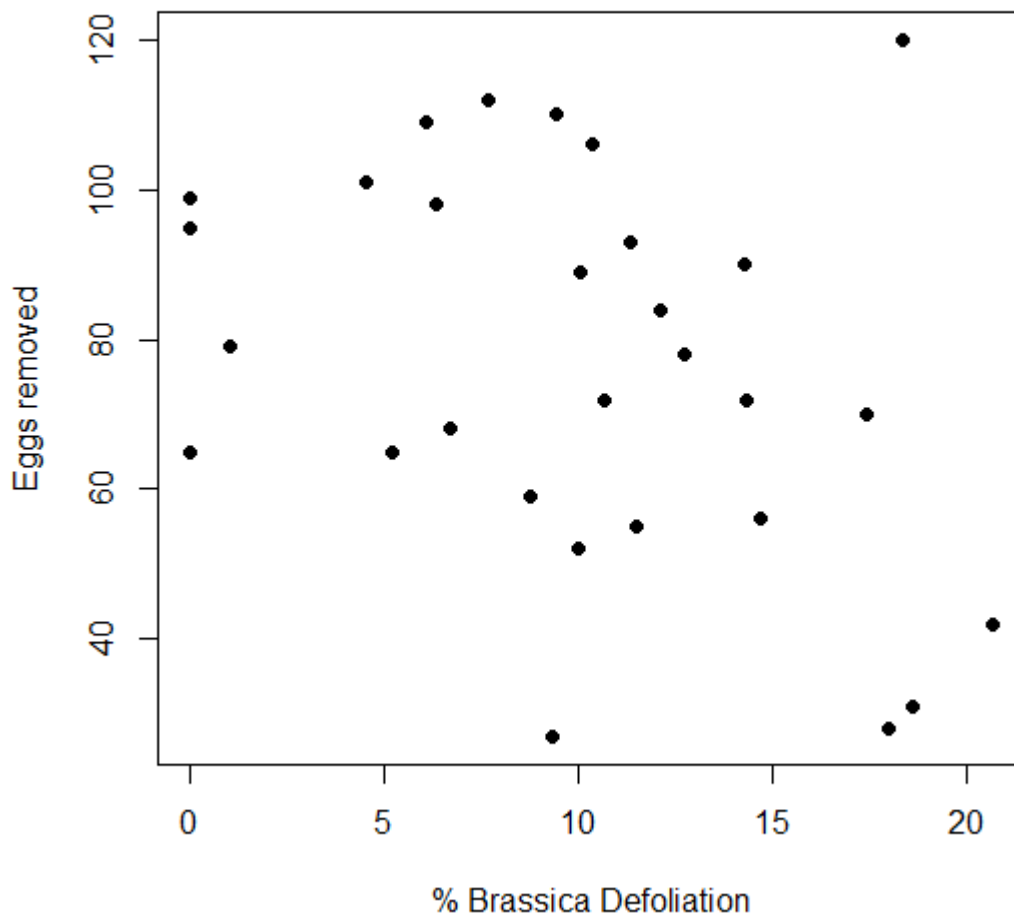


Figure 6. Model selection identified a weak negative relationship between cabbage looper egg suppression and percent defoliation of brassica (refer to text). The initial number of larvae at each site was between 144 and 155.

## APPENDICES

### Appendix A. IRB approval 2013-1142 for material used in Chapter 1.

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November 25, 2013

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